The University of Chicago

STUDIES IN PALEOZOIC CORALS

AN EXPANSION OF A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE PHYSICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY
1934

By
BRANDON H. GROVE

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STUDIES IN PALEOZOIC CORALS

BRANDON H. GROVE

I. Introduction

During the past century our knowledge of corals has been built up from the contributions of many men in many lands. The complete picture thus constructed, however, can only be perceived when its various units have been translated into a common tongue and presented as a coherent whole. A critical review of this sort was made by Jules Haime in 1860, in the first volume of Milne-Edwards' *Histoire Naturelle des Coralliaires;* and the studies of the following decade were similarly summarized by De Koninck in his *Animaux Fossiles du Terrain Carbonifere de la Belgique.* (1872). The years subsequent to De Koninck's writings have probably been those most significant in the study of corals, but few authors have paused to summarize the numerous data resulting from these researches, and, further, the best of these exacting surveys have been made in languages other than English.

It is hoped, therefore, that the historical summary offered in Part I of the present paper will prove of value (1) in presenting the general data available to modern students, (2) by indicating the sources of detailed studies for those interested particularly in restricted fields, and (3) by offering a brief survey, in English, of the many works available only in foreign tongues.

I am indebted to Professor Carey Croneis, of the University of Chicago, for suggesting the present study, and for his continued counsel and guidance in the present work. My sincere thanks are also due to Mr. A. W. Slocum, of Walker Museum, University of Chicago, whose suggestions in the matter of technique have been invaluable, and to the curators of Walker Museum, who have made available the splendid examples of Mississippian corals afforded by the Miller, Sampson, Weller, and Gurley collections.

II. A Summary of Modern Studies in the Paleontology of Corals

Introduction of Modern Technique

Laurent De Koninck, penning the introduction to his *Nouvelles Recherches sur les Animaux Fossiles,* published in 1872, expressed deep regret that he

was unable to avail himself of the results of the newly inaugurated study of corals by means of their thin sections. This study was then in the hands of committee appointed in 1868 by the British Association for the Advancement of Science. Monsieur De Koninck politely expressed the hope that the skill and ardor of the committee, composed of James Thomson, Henry Woodward, and R. Harkness, would more than suffice to overcome the great technical difficulties of their task. His apprehensions regarding the complication of the work, however, seem to have been well founded, for in his first report to the British Association, in 1869, James Thomson had announced that although several hundred corals had been sectioned, most of them had been so crushed and fractured that they were useless for their purpose. Indeed, in one lot of eighty-seven corals, only two sections were sufficiently perfect to warrant being photographed. The time and labor involved in the cutting, examining, and finishing of sufficiently perfect sections made it impossible to produce a complete set within a year. In addition, the photographs themselves, made by the then current process, soon faded upon exposure to light. Therefore the hope was expressed that a new carbon process would be an improvement, and also that they might soon be able to produce fac-similes on zinc or copper plates.

During the second year of the committee's existence it made much greater progress, and at the meeting of the British Association in 1870 it exhibited nine photographic plates presenting sections of the genera *Amplexus, Zaphrentis, Cyathophyllum, Campophyllum, Clisiophyllum* and *Cyclophyllum*. Referring to this latter genus, the committee emphasized the importance of employing thin sections in the study of corals by the following statement:

> "The history of this specimen is perhaps one of the best illustrations on record showing the necessity of carefully working out the details of fossil corals before they receive either generic or specific names. It was named *fungites* by Ure in 1793, *Turbinolia fungites* by Fleming in 1828, *Cyathophyllum fungites* by Geinitz in 1845, *Clisiophyllum prolapsum* by McCoy in 1849, *Aulophyllum fungites* by the same authors in 1851 who named it *Aulophyllum prolapsum* in 1845, viz. Milne-Edwards and Haime. This great diversity of nomenclature we can only attribute to the fact that non-essential and external characteristics have been too implicitly trusted in drawing generic distinctions; when we examine their internal structures, genera named exhibit essential differences of conformation" (1870, pp. 43-44).[1]

In its third report, in 1871, the committee again emphasized the difficulty it was meeting in the too frequent crushing and fracturing of its specimens during the processes of cutting and grinding. It announced, however, that much better results had been achieved in photography, and that it had been successful in transferring even the finest details of the sections to copper plates, making them available for extensive publication in the future.

By 1872 this careful study and comparison of the internal characters of hundreds of specimens was beginning to bear fruit in other than purely technical ways. The report of the committee for this year contains a lengthy morphological study, with recommendations as to which of the structural fea-

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1 References are given by means of the chronologic position of the work cited in the alphabetic list of authors to be found in the bibliography at the close of the paper.

tures of corals were of probable generic and specific significance. The presence or absence of a columellarian line, and of endothecal dissepiments, were considered inadequte for specific determinations. Among the 156 established species of British fossil corals, they found the existence of between 300 and 400 varieties, the increase in the number of varieties over those previously known being so great, and the variations so minute, that they found difficulty in determining just what constituted specific characters. Their conclusions regarding this difficulty, and their suggestion for a solution, are of some interest:

"The gradations of the varieties are in some cases so constant, and pass so imperceptibly into each other, that they induce the inference that there has been an inherent tendency in the polyp to vary independent of, but to be modified by, the conditions of its surroundings. . . . In order that some definite rule may be obtained as a guide in the classification of corals, it is proposed to select generic types, and, after making sections of these through different parts, to exhibit their structure in plates, from the ova to the mature form; and it is only when this is faithfully done that we can hope to determine where a species begins and a variety ends." (1872, pp. 242-243).

The British Association was sufficiently impressed with the importance and potentiality of the work to continue its grant to the committee, and to augment its numbers by the appointment of Thomas Davidson and P. Martin Duncan, the latter of whom had just completed his important monograph on the Tertiary corals of Great Britain.

In its fifth and final report, in 1873, the committee exhibited an extensive series of plates showing serial sections of a wide variety of genera, but dealing particularly with species and varieties of *Zaphrentis* and *Amplexus*. James Thomson was assigned the task of publishing and elucidating the data and plates resulting from these five years of research by the committee.

Although hardly of more than secondary importance in itself, this work of the British Association's committee merits thoughtful recognition, not merely as a pioneering effort in the use of thin sections, but because it marks the introduction of modern scientific method into the paleontology of corals. So long as workers confined their attention only to form and features visible externally they dealt with ephemeral characteristics, susceptible only to general description. With the introduction of the exact data afforded by serial sections, however, there came the possibility of truly scientific discussion of ontogeny and phylogeny, morphology, and taxonomy, and the accurate comparison and delineation of genera, species, and varieties. The paleontology of corals came a step closer to being an exact science.

Morphological Studies

While the British scientists were thus engaged in shaping a new tool for the study of corals, the morphological discoveries of the French and German workers were preparing the way for its efficient employment. The labors of A. Kunth, in Germany, were of outstanding significance in this respect. To Kunth we owe the recognition of the mode of septal insertion peculiar to the tetracorals, formulated in the law which bears his name. (1869). Prior to

Kunth's studies it was not recognized that tetracorals differed from hexacorals in the manner in which new septa were added with continued growth. In fact the general rules for septal insertion worked out by Milne-Edwards and Haime, (1860, vol. I, pp. 48-51), were assumed to be equally valid for both the Tetracoralla and the Hexacoralla. As can be seen from the diagram of figure 1, the septal scheme of Milne-Edwards and Haime is based upon the assumption of radial symmetry in all corals, and the postulation of six primary septa. New septa are then inserted in groups of six, or multiples of six.

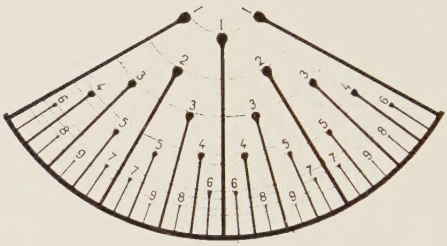

Fig. 1. Scheme devised by Milne-Edwards and Haime for septal insertion in corals.

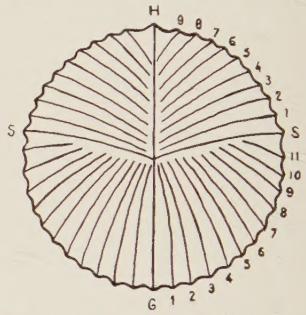

Fig. 2. Method of septal insertion in the Tetracorals according into Kunth.

The researches of Kunth showed for the first time that the arrangement of the septa among the tetracorals is not in acordance with a radial, but with a bilateral symmetry. He thus made available a criterion of the highest morphological value, for this disposition of the septa is characteristic of all the tetracorals, and stamps them unmistakably.

Kunth reached his conclusion largely by making a careful study of the stripes or ribs reflected onto the external portion of the corallum by the septa, but a similar conclusion can be drawn from a study of the arrangement of the septa within the cup itself. In a diagram of figure 2, the lines *h, s, g,* and *s* represent the four primary septa of a tetracoral. In the absence of other data, they may be recognized by the fact that the lines which they reflect upon the exterior of the cup extend all the way to the tip, showing that these septa were formed in the very earliest stages of growth. Of these four primary septa, *h* is designated the *cardinal septum, g* the *counter septum,* and both the septa designated as *s* are *alar septa;* the two quadrants of the cup which lie between the cardinal septum and an alar septum are called cardinal quadrants, and those enclosed by an alar septum and the counter septum are called counter quadrants.

In the light of these definitions, Kunth's law of septal increase may now be expressed as follows: In the cardinal quadrant all the secondary septa originate ajacent to the cardinal septum, and in time take up a position parallel to the alar septa; on the other hand, in the counter quadrants all the secondary septa originate adjacent to the alar septa, and take up a position parallel to the

counter septum. As a result, in the cardinal quadrants the secondary septa lying next to the cardinal septa are the youngest, and those lying closest to the alar septa are the oldest. In the counter quadrants the oldest secondary septa lie next to the counter septum, and the youngest are closest to the alar septa. There is thus a bilaterally symmetrical septal arrangement.

The fundamental importance of Kunth's discovery was greatly enhanced by the introduction of the technique of serial sectioning, which permitted a detailed study of the initial stages in the growth of a coral, and thus allowed the fullest application of morphological knowledge. An even deeper insight into the initial stages of coral development was given by the accurate studies of Lacaze-Duthiers upon living corals. In consequence of his research upon Actinarians, this author was able to publish, in 1872 and 1873, a survey of the earliest events in the secretion of a corallum and the development of the septa. (1872, 1873).

Lacaze-Duthiers introduced his studies by reviewing the works of the more important writers who had preceded him, notably Milne-Edwards and Haime, Schneider and Rötteken, and C. Semper. He concluded that in the writings of each of these authors there existed a common weakness. With each of them the interpretation of the sequence of events occurring in the development of a coral was based upon the relationship of its parts at the time of observation. From studies of this sort Milne-Edwards and Haime, and Schneider and Rötteken, had gained the belief that septa originate in cycles, of successively younger orders, and had worked out elaborate rules to account for this cyclic insertion of septa. Semper, who studied living forms, cast some doubt upon this conception by showing that it was subject to numerous exceptions, but he did not attempt to refute it. After a prolonged study of the development of both soft and stony corals, from the embryo to the adult form, Lacaze-Duthiers found that in neither the formation of the mesenterial folds, nor in the secretion of the calcareous septa, was there any simulation of a cyclic mode of development. Both mesenteries and septa arose progressively, and the apparent arrangement of these and the tentacles into successively younger orders arose in consequence of predetermined limitations in the extent of their growth.

The development of the mesenteries and the formation of the calcareous parts, as determined by Lacaze-Duthiers, may be briefly outlined as follows: The first differentiation of the visceral cavity of the embryo takes place with the formation of two oppositely placed mesenterial folds, which divide the cavity into two unequal sectors. In the larger of these sectors two new mesenteries arise and divide it into three compartments; shortly thereafter the smaller sector is similarly subdivided by a pair of mesenteries. This alternate insertion of pairs of mesenteries continues until the total number possessed by the animal is achieved, regardless of how large this number may be.

The first deposits of calcite appear when the mesenteries have divided the visceral cavity into twelve compartments. The secretion of calcite takes place within the inner wall, the endoderm or endothelium. The septa are

the first parts to be so formed, and their genesis takes place nearly simultaneously in each of the twelve triangular compartments formed by the junction of two mesenteries with the wall. The deposition of calcite nodules or scleres arises from three centers of secretion in each compartment, one such center being located in each corner of the triangle. With continued growth the two peripheral deposits elongate toward the central one, which advances to meet them, until with their conjunction a Y- or V-shaped arrangement is produced. (Fig. 3). It is not until the formation of the septa is well advanced that the calcification of the wall and base of the coral begins, and when this has progressed sufficiently, the two arms of the septal V coalesce with the wall. The development of a columella does not begin until after the septa have reached this stage.

As the deposition of calcite continues, six alternate septa continue to be enlarged for a considerable time after the other six have reached their full dvelopment, and the difference in size thus produced leads to the appearance of two cycles of septa, of unequal size.

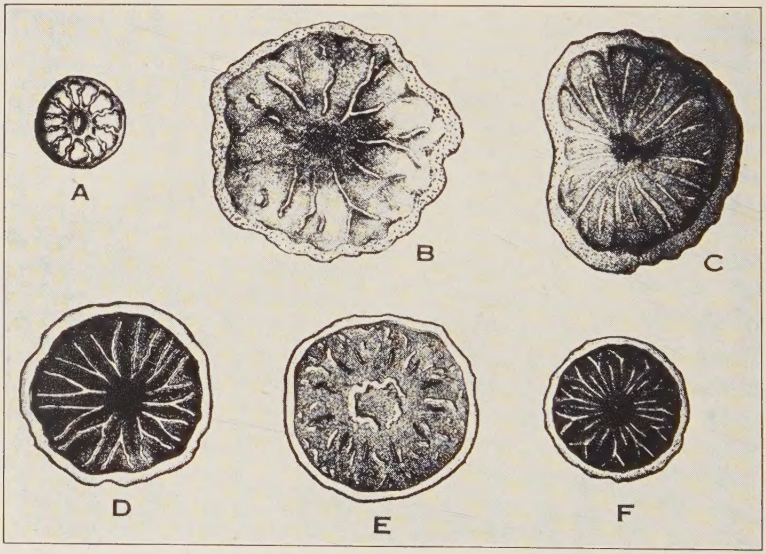

Fig. 3. Some early stages in the formation of the calcareous septa in *Asteroides calycularis*. (After Lacaze-Duthiers).

The stages of development outlined in the foregoing are those observed by Lacaze-Duthiers in the Mediterranean coral, *Asteroides calycularis*, and verified by him upon a number of other forms. It is unfortunate that he was unable to make precise observations beyond the stage in which twelve septa were developed, but his results are none the less significant.

Dybowski's Classification

Concurently with the morphological studies of Kunth and Lacaze-Duthiers two writers of northern Europe were making important contributions to taxonomic and phylogenetic knowledge. Lindström, in Sweden, was already recognized as an authority of fossil corals, although he had not yet published his researches upon the operculated corals, which climaxed his works, and which will be discussed later; and Dybowski, in 1874, published his monograph on the Silurian corals of the Baltic Provinces of Russia.

Dybowski studied corals by means of vertical and transverse thin sections, and he was the first to announce a verification of Kunth's law. While the greater part of his monograph is devoted to the description of new genera and species, its principal importance lies in the presentation of an advancement in the classification of the tetracorals. Dybowski perceived that the entire group Tetracoralla could be divided morphologically into two families, which he named *Inexpleta* and *Expleta*. The two families are very unequal in the number of forms they embrace, the *Inexpleta* being a rather modest group numerically, characterized by the general absence of endothecal structures, while the *Expleta*, which are defined by the existence of tabulae and dissepimental tissue, include the majority of the tetracorals. The advantages of this classification, aside from the fact that the morphology of the forms demands it, is in the analogy it presents with the Hexacoralla, whose principal systematic subdivisions are likewise based upon the nature of the endothecal structures. A further interesting fact brought to light by this grouping is the marked parallelism existing between the *Expleta* and the *Inexpleta*, in consequence of which individual subdivisions of the former are exactly analogous to those of the latter. Thus the Inexpletan *Cyathaxonidae*, *Petraiidae*, and *Polycoelia* find their counterparts in the Expletan *Axophyllidae*, *Zaphrentidae*, and *Cyathophyllidae*.

The broader features of Dybowski's classification have won wide-spread acceptance, and are now in general use; his descriptive and morphological work, however, has frequently been subjected to sharp criticism, especially at the hands of Lindström.

Very shortly after the appearance of Dybowski's monograph still further revision of the existing classification of corals was urged by M. G. Dollfus, in a paper read before the Academy of Sciences, in Paris. (1875). Dollfus suggested the division of the *Rugosa* into two classes, the first of which should include those Paleozoic corals having an irregular septal system, with the septa always free, and with or without tabulae. (In general the *Zaphrentinae* and *Cyathaxoninae* of Edwards and Haime). The second class would embrace those types having a regular septal system, with the septa arranged in variable fashions. Since Dollfus argued for the abandonment of the tetrameral character of grouping the septa, the members of his second class would be distinguished from the *Zoantharia aporosa* only by the presence of tabulae. Dollfus lamented the fact that the group *Tabulata* had become merely a dumping ground for poorly known forms; and, in urging its revision, he

presented a series of phylogenetic relationships which he believed could be traced between the tabulates and modern forms. Briefly, the relationships he suggested are:

The Heliolitidae *(Lyellia, Propora),* are the ancient representatives of the modern millipores, through the intermediation of the Pocilliporidae *(Pocillipora, Axopora, Polytremacis).*

The Syringoporidae *(Syringopora, Fletcheria, Halysites,* etc.), correspond either to certain Bryozoa *(Hypothoa, Idmonea),* or to certain tubulose Alcyonaria.

The Chaetetidae with perforate walls *(Stillipora, Chaetetes, Dania, Beaumontia, Labechia, Dekaya)* offer a direct parentage to the Jurassic Bryozoans of the group *Heteropora,* and to the Cretaceous Bryozoa *Radiopora.*

The Favositidae are directly ancestral to the tubulose Bryozoa *(Cyclostomata),* and the *Dendroporidae* have a similar relationship to the Bryozoa of the group *Hornera.*

Dollfus was content to offer merely criticism and suggestion, and made no effort to set up a detailed classification.

Work of Thomson and Nicholson

Meanwhile, in England, J. Thomson and H. A. Nicholson, the heritors of the extensive material resulting from the five years of study by the British Association's committee on Carboniferous corals, began the publication of their results from the study of this material. The first of these papers was by Nicholson, (1875), and in it he recognized the following modes of growth among Paleozoic corals:

A. *Simple calicular gemmation,* in which the corallum sends up from its calicular disc a single bud, which usually repeats the process, until there is produced a succession of corallites vertically superimposed. This mode is peculiar in that the same calice never produces more than a single bud.

B. *Compound calicular gemmation.* Two or more buds are thrown up from the primitive oral disc, and these commonly repeat the process in turn, until the corallum forms an inverted pyramidal mass, composed of numerous corallites diverging from the base.

C. *Parietal or lateral gemmation.* The corallum increases by the production of buds at some point in the walls of the parent corallite between the lip of the calice and the base.

D. *Basal or marginal gemmation.* New corallites are produced at the circumference of the colony, or along certain definite lines proceeding from the base.

E. *Fission.* The growth of the corallum is effected by the cleavage of the calice of the original corallite or corallites.

Nicholson concluded that little stress could be placed on mode of growth as applied to the classification of Paelozoic corals. He found that allied forms of the same genus, and even different individuals in the same species, show entirely different modes of growth. On the other hand forms belong-

ing to the most remotely related groups often increase in the same way. The common difficulty in recognizing the mode of growth in any particular specimen is a further barrier to the use of this characteristic for classificatory purposes.

The most important fruits of Nicholson's and Thomson's studies appear in a series of papers published during the year 1875. These deal with the recognition of the principal generic types of Paleozoic corals. (Nicholson, 1875a, Thomson and Nicholson, 1875). After stressing the use of serial thin sections as the only possible scientific method for the study of corals, the authors urge, as a basis for classification, the adoption of elastic generic types, rather than a continuance of efforts to isolate genera by rigid definitions. Since Thomson and Nicholson were in possession of unusually abundant data, their argument in favor of generic types is proportionally important, and is here given:

"As investigated by the method which we have employed, the corals of the Paleozoic period very strongly support the view that they owe their structural peculiarities to some form or another of evolution. Whenever a sufficiently large number of specimens of any given group can be obtained and submitted to examination by means of sections, a complete passage is usually found to exist into other allied groups. So complete is this transition, and so gradual are the steps by which it is effected, that it becomes impossible for the most painstaking observer to draw any hard and fast line of demarcation between such inosculating groups." (Nicholson, 1875a, p. 307).

In keeping with the conclusion thus expressed, Thomson and Nicholson undertook the description of a number of such generic types, giving complete descriptions of the external and internal characters and the relationships of the forms selected. Included as type genera are *Amplexus*, *Zaphrentis*, *Cyathophyllum*, *Campophyllum*, *Diphyphllum*, *Lophophyllum*, *Lithostrotion*, *Koninckophyllum*, *Lonsdalia*, *Clisiophyllum*, *Dibunophyllum*, and *Aspidophyllum*.

Among the many important contributions to the paleontology of corals appearing in the year 1875 must also be included the description of the Mesozoic corals of the Nattheimer strata, by Becker and Milasewitch. (1875). This lengthy work is primarily of value for the new material which it brings to light, for aside from a discussion of classification, it contains little of a general nature.

Hall and Rominger

The appearance, in 1876, of Carl Rominger's description of the fossil corals of Michigan marks the first important contribution from North America. (1876). During the same year James Hall published his illustrations of the Devonian corals of New York State. Rominger's work contains both descriptions and illustrations, whereas that of Hall is little more than a compilation of plates. In the manner in which they handle their material the American authors are quite antiquated. They are apparently unaware of much of the work which has been done in Europe prior to their publications, and Rominger's descriptions are modelled after those of Edwards and Haime, rather than Thomson and Nicholson. Neither work exhibits any attempt to

use thin seections, either in the ilustrations or in the actual study of the material. The importance of these volumes rests almost entirely on the depiction of new genera and species, as both pioneer into the hinterland of hitherto scarcely touched North American material.

Morphology of G. von Koch

In 1879 G. von Koch published in Germany the first of an important series of morphological papers containing the results of his observations upon both reef and cup corals. In this paper he concluded that the *theca* or wall of the corallum arose from a thickening and fusion of the distal ends of the septa, and not, as had been previously supposed, from a continuation of the foot secretion responsible for the calcification of the base. Von Koch availed himself of the most scientific methods of research known to his time; and in addition to the use of serial thin sections, he introduced an innovation in the use of trasmitted light as a means of detecting variations in the mode of deposition of the calcitic sclerites and nodules revealed in his sections. With the help of this latter tool von Koch analyzed coral skeletons, and classified them as follows: (1882).

A. Skeleton formed of minute free spicules.
   1. Individual corals *(Alcyonaria)*.

B. Skeleton formed partly of fused spicules and partly of crystalline material.
   1. Corals with compound skeletons.
      a. Skeleton secreted by individual polyps; theca formed from the cementing materials of the body; never possess eight true septa. *(Tubipora* and probably *Heliopora,* most *Tabulata)*.
      b. Theca an independent structure; true septa present. (Most recent *Madreporaria perforata* and *aporosa)*.
   2. Individual polyps united by a coenenchymal tissue.
      a. Colonial forms with skeletons composed of fused spicules. *(Corallium, Mopsia,* etc. No fossil forms).
      b. Forms possessing a horny or more or less calcified skeleton secreted by the ectoderm of the coenenchyma. *(Gorgonides, Pennatulides. Isis* is the only known fossil form).

The most important of von Koch's papers, however, appeared in 1883, and dealt with his observations of sexless reproductive methods among Paleozoic corals. (1883). Although his results seem in general to conform with those of Nicholson's earlier study, previously discussed, the work of von Koch is much more precise, and permits a much clearer conception of the successive morphological changes involvel in the formation of young corallites from the parent calyx. As classified by von Koch, a-sexual reproductive methods of Paelozoic corals fall into two general groups, which he names *Internal Budding* and *External Budding*. Under the first of these he includes the following types:

A. *Fission budding.* The wall and endothecal apparatus of the mother calyx are directly transitional to the daughter calyx, without any alteration. The separation of the two results simply from a fusion of the two oppositely lying points of the calicular wall of the parent. (Fig. 4, a).

B. *Septal budding.* The parent calyx becomes subdivided into two or three, or rarely four, buds. A part of the original wall and its septa are transitional to the bud, but an essential part of the wall of the bud is formed from an envelopmental curving of the four primary septa. (Fig. 4, b). This type of reproduction is found in the genus *Stauria.*

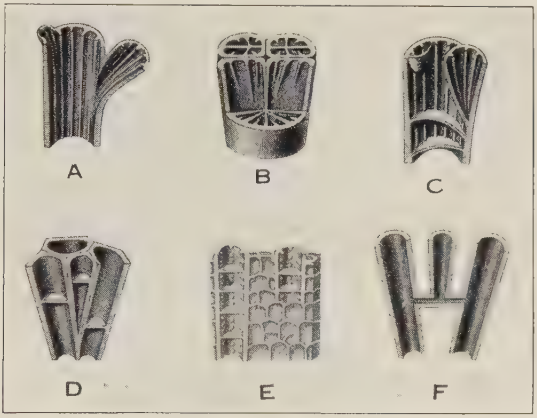

Fig. 4. A sexual reproductive forms. (After von Koch). (a) fission budding. (b) septal budding. (c) tabular budding. (d) interstitial budding. (e) coenenchymal budding. (f) stolon budding.

C. *Tabular budding.* In this type of reproduction the young calyx originates partially from the wall of the one already existing, and becomes completed through a pocket-like bending of a tabula. *Acervularia, Fascicularia, Amplexus,* and *Pholidiphyllum* exhibit this method. (Fig. 4, c).

D. *Interstitial budding.* The mother calyx takes no visible part in the formation of the bud, which appears entirely independently in the interstices between the older calices. *Favosites* and related genera demonstrate this form of increase. (Fig. 4, d).

E. *Coenenchymal budding.* This form of budding is similar to the interstitial budding of the Favosites, except that in it the new calyx arises in the coenenchymal tissue. The bud may be more or less of a continuation of preexisting lamellae in the coenenchyma, or it may be an entirely new structure. This form of budding is shown by *Heliolites,* the modern *Heliopora, Plasmopora, Galaxia,* and analogous forms. (Fig. 4, e).

F. *Stolon budding.* The visceral cavities of the individual corallites are

connected by a tube or stolon. The new bud is formed by the continuation of the walls of the stolon as walls of the infant calyx. (Fig. 4, f). *Syringopora, Syringophyllum,* and the modern genus *Tubipora* exhibit this type of budding.

In addition, von Koch recognized a reproductive form which he termed *rejuvenation,* in which the new calyx is identical with the old one, which becomes constricted and reduced in size, but does not alter otherwise.

Zittel

The year 1879 is made noteworthy by the appearance of Karl A. von Zittel's *Handbuch der Paläontologie.* This work has since become so widely known as a standard reference text for general Paleontology that it is hardly necessary to give here more than a brief notice of Zittel's treatment of corals. The essential purpose of the writer was systematic classification, and his grouping of the corals is a synthesis of what he considered the better features of the existing classifications. Thus, his order *Zoantharia* and sub-order *Madreporaria* are taken from the classification of Milne-Edwards and Haime, but in placing under this sub-order the groups *Tetracoralla* and *Hexacoralla* he follows Haeckel. In subdividing the tetracorals he chose Dybowski's families *Expleta* and *Inexpleta,* and he followed Dybowski further in partitioning the latter family into the sub-families *Diaphragmatora, Plenophora,* and *Cystophora.*

Zittel's classification of the hexacorals is similarly composite, the majority of the divisions being adopted from the work of Milne-Edwards and Haime. In his treatment of the tabulates, he is most revolutionary, however, for he entirely abolishes the group, and disposes of its members in a variety of ways. *Millepora,* and allied forms, and *Labechia,* are placed in the *Hydrozoa;* the entire family of the *Favositidae* is assigned to the hexacorals as a subdivision of the *Poritidae;* a second sub-family of the *Poritidae* is formed by *Koninckophyllum* and *Alveopora; Syringopora, Aulopora, Halysites,* and their relatives are placed in the *Alcyonaria,* in the family Tubiporidae. The *Chaetetidae* are entirely removed from the *Anthozoa,* and placed in the *Bryozoa* under the order *Cyclostomata.*

Very shortly after the publication of the Handbuch, Zittel's dispersal of the tabulates received strong support from H. A. Nicholson in a book devoted entirely to a discussion of the *Tabulata.* (1879). In this work Nicholson corroborated the views of Verril and Lindström as to the necessity of abolishing the *Tabulata* as a distinct and separate subdivision of the *Zoantharia,* and concluded that under the old name "Tabulata" there are included at least twelve distinct groups of corals. For the purpose of his book, however, he retains the tabulates as a unit, and discusses them under the families *Favositidae, Columnaridae, Syringoporidae, Auloporidae, Halysitidae,* (and *Tetradiidae*) *Thecidae* (and *Helioporidae*), *Chaetetidae, Monticuliporidae,* and *Labechidae.*

Nicholson further augmented his studies of the tabulates by publishing, in 1881, a treatise devoted entirely to the genus *Monticulipora.* The avowed

purpose of this lengthy quarto volume is not so much to determine the systematic position of *Monticulipora* as to describe and figure the genus in such detail that its species might always be readily and accurately determined. The incentive to the work was given by Nicholson's disgust with correlations of strata made over wide areas on the basis of species whose determination from the existing descriptions he considered impossible.

An important contribution to the knowledge of modern corals was made in 1880, when C. B. Klunzinger, a German physician and naturalist who lived for many years on the shores of the Red Sea, published his observations of the coralline forms of that region. In his three volume work he suggests many changes in the classification of Milne-Edwards and Haime, and gives in addition a valuable series of photographic plates. (1877-1879).

The return of the Challanger expedition, in 1880, brought even greater additions to the data on modern corals. H. N. Moseley, in his report on the zoological studies of the expedition, verified Dana's contention that the affinities of the Millepores were with the Hydrozoa, and thus finally removed this group from that of the corals proper. (1881). Moseley also devoted a great deal of study to the modern genus *Heliopora*, and he concluded that the fossil genus *Heliolites* is transitional between the present-day *Helioporidae* and some such ancient form as *Favosites forbesi*. In this he directly contradicted the previously mentioned postulation of Dolfuss.

Lindstroem

Gustave Lindström, of Sweden, whose position of authority in regard to the Paleontology of corals has already been noted, published in 1882 his extremely important treatise on the operculated corals. This paper, which is characterized by its thoroughness, is an inclusive discussion of the *Operculata*, tracing the genesis, relationships, and mutations of the group. Lindström divides the operculates into two families, the *Calceolidae* and the *Araeopomatidae*, the former containing the genera *Goniophyllum*, *Platyphyllum*, *Rhizophyllum* and *Calceola*, and the latter the genera *Areopoma* and *Rhipidophyllum*. He sees as the immediate ancestor of the group a mutation of *Goniophyllum pyrimidale*, found at the base of the upper Silurian. Near the close of the late Silurian the group has reached its maximum expansion, and is represented by all of its genera except *Calcola*. In the early Devonian the genus *Rhizophyllum* is the only representative of the group, and *Calceola* of the late Devonian is considered its direct descendant.

Structural Studies of Pratz and Frech

Another important paper appearing in the year 1882 was that of E. Pratz, who studied the septal structure of a number of hexacoral genera, and endeavored to group and relate their forms on the basis of peculiarities in their septal structure. Pratz confined his researches to the fossil members of the *Fungidae*, and he was able to divide the family into four groups, each of which showed distinctive types of septal apparatus. As identifying characters, he used the manner of deposition of the sclerenchymatic substance, the arrangement of the trabiculae, and the presence or absence of synapticulae and

endothecal traverses. He showed that traverses could not be considered as morphological substitutes for synapticulae, since both occurred in the same specimen at times, and he attempted to distinguish between true synapticulae and pseudo-synapticulae, the latter of which he explained as resulting from the union of two trabiculae.

In 1885, Frederich Frech, also a German, published the first of several papers dealing with the middle and upper Devonian corals of Germany. The bulk of Frech's work is devoted to the systematic description of genera and species, (1885, 1886), but one paper is given entirely to a consideration of the skeletal structure and relationship of the tetracorals. (1885a).

In analyzing the structure of the septa, Frech reviews the positions of Dybowski and Kunth, who held that the septa of tetracorals were composed of two parallel lamellae, and that of Lindström, who maintained that but a single lamella was involved in each septum. To this Frech adds his own observation on *Streptelasma,* in which he finds the septa to be formed from infoldings of the outer wall of the corallum. He concludes that each of these three types of structure, and many intermediate modifications of them, may be found among corals of different genera; and that the most common type of septal structure among Paleozoic tetracorals is that depicted by von Koch, in which the septum proper is but a shadowy blade, completely covered by deposits of structureless calcareous material which he named *stereoplasma.*

In regard to the theca, or inner wall of the corallum, Frech finds that ontogenetically and histologically it seems to be composed of the same elements as the septa; in many cases merging with the stereoplasma of the septa without any visible line of demarcation. He concludes from this that the outer wall of the corallum in tetracorals is the theca, and objects to the prevailing use of the term "epitheca" to designate it.

After comparing the skeletal structure of the tetracorals and the hexacorals, Frech says:

> "On zoological grounds it is scarcely possible to rebuff the conception that the *Tetracoralla* may have been the stem ancestors of the *Hexacoralla.* Their geological appearance speaks also for this hypothesis. The 'recoining' appears to have taken place during the period in which the Bunter sandstones were formed. The few Permian forms still belong decidedly to the tetracorals, whereas the genera known from the Muschelkalk and the Alpine Triassic are related to living forms, although, to be sure, the hexacorals still have a somewhat ancient stamp." (1885a, Writer's translation, p. 942).

In 1885 P. Martin Duncan undertook the first important revision of the *Madreporaria (Zoantharia Sclerodermata)* since their classification by Milne-Edwards and Haime. Duncan confined his attention to the broader subdivisions, and excepted the *Rugosa* from consideration. (1885). His suggested revision is as follows:

Order *Madreporaria*
Sub-order *Aporosa*
Family I. *Oculinidae*
II. *Pocilliporidae*
III. *Astraeidae*
IV. *Turbinolidae*
Sub-order *Fungida*

Family I. *Pleisiofungidae*
II. *Fungidae*
III. *Lophoseridae*
IV. *Anabaciadae*
V. *Plesioporitidae*
Sub-order *Perforata*
Family I. *Eupsammidae*
II. *Madreporidae*
III. *Poritidae*

Duncan abolished the sub-order *Tubulosa* of Edwards and Haime, in the belief that its members are not true corals. The sub-order *Tabulata* (E. & H.) is likewise broken up and its members distributed.

The enduring work of Thomson and Nicholson, in England, was continued in 1883 with the appearance of a paper by Thomson dealing with the corals of the Carboniferous of Scotland. (1883). Thomson's object was to illustrate the evolution and close interrelationships of the genera and species he studied, and in a number of respects his paper is revolutionary. For example, under the heading *Hydrozoa* he unites such presumably diverse genera as *Aulopora, Michelinea, Chaetetes, Zaphrentis, Amplexus, Favosites, Syringopora,* etc. As *Zoantharia rugosa* he groups *Diphyphyllum, Lithostrotion, Cyathophyllum, Lonsdalia,* and others, and in *Actinozoa rugosa* are placed *Cyathaxonia, Lophophyllum, Axophyllum, Aulophyllum,* etc.

Thomson chooses the simple and structureless genus *Aulopora* as a starting point for his attempt to trace the interrelationships which he believes must exist in all the genera studied, as a consequence of their evolutionary development. The first developmental step from *Aulopora* is *Cladochonus,* which is likewise nearly structureless, but which has a thin zone of vesicular tissue around its inner wall, and in this Thomson sees a transitional character toward *Syringopora.* The tabulae of *Syringopora* are considered as foreshadowing *Michelinia,* while its peripheral vesicular zone is seen as a forerunner of the broad vesicular zone of *Thysanophyllum.*

In a similar way all the species of the Scottish coral genera are analyzed on the basis of their structural changes, the final result being an evolutionary linking of all the species studied. In many cases the transitions postulated seem clear and probable, but in others the gaps are not so easily bridged, and the work is abundantly open to the criticism of future observers.

Of some importance to morphology is E. von Marenzeller's study of the genus *Flabellum,* published in 1887. In this work is found the first careful observation of the phenomenon now generally known as "septal acceleration." Marenzeller noted that in some species of *Flabellum* the interseptal chambers at either end of the long axis of the corallum seemed especially favored for the addition of new septa, and septa of a higher order appeared here before those of the next lower order had been formed in the other chambers. He also observed that in every species the evolution of septa of the higher orders proceeds irregularly, and that the septa of the first three orders tend to become equal in size through the continued growth of the later ones. Marenzeller was able to divide the genus *Flabellum* into three major groups on the basis

of the number of septa in a cycle, and the rate and ratio in which these were inserted.

Concurrently with the above-mentioned work of Marenzellar, G. von Koch published another of his important morphological studies. (1886). In this he discusses the coral skeleton in its relation to the soft parts of the body. Of particular importance are his subdivisions of the skeleton, which are here given:

I. *The Basal Plate.* This separates the arboreal end-surface of the soft body from the underlying surface which holds the skeleton erect. Its form is to a high degree dependent upon the form of the supporting surface, but in general it may be said to be flat and circular.

II. *The Outer Plate.* (Epitheca). A continuation of the basal plate, more or less distinctly set off from the latter, and covering the body wall upon the outside. Among most corals the outer plate is conical in shape.

III. *The Inner Plate.* (Theca). This has generally a ring shape, and projects upward from the basal plate parallel to the soft body walls, becoming covered by in-foldings of these latter. Since many such folds may be laid on concentrically, there may thus be a number of inner plates in a given individual.

IV. *Radial Plates.* (Septa). These plates form radial walls rising vertically from the basal plate, and lying within radial folds of the body wall. They exist in the majority of corals.

William Waagen, as part of his many years of study of the invertebrate forms of the Salt Range of India, published in 1886 and 1887 his description of the corals of the Productus limestone of that region. He devoted the greater part of his large volume to the descriptions of new genera and species from this hitherto little known area, but in a number of cases he attempted to bring his material to bear on the solution of morphological or phylogenetic questions then in dispute. The most important effort of this kind occurs in his study of the genus *Monticulipora*, in regard to which Waagen sided with Nicholson, holding it to be a coral, as opposed to Lindström and Rominger, who considered it a *Bryozoan*. As a basis for his point of view, Waagen offered his discovery of a type of gemmation peculiar to the *Monticuliporidae*, which he named "Intramural Gemmation." In this mode of growth the new corallite is produced by a splitting of the primary mural plates of two or more adjacent corallites, which first become thickened, and then divide in half to furnish the walls of the new bud.

Waagen found that tetracorals are very sparsely represented in the Productus limestone, but that hexacorals of the tabulate type abound. He considered the Paleozoic age of the hexacorals to be conclusively proved by the relationship of the *Favositidae* to the *Poritidae*.

Neumayr

In 1869 there appeared the first volume of M. Neumayr's "Stämme des Thierreichs," a work probably of more importance to general Paleontology than any since the publication of Zittel's "Handbuch." Unlike Zittel, Neumayr did not aim at systematic classification, but attempted rather a

general survey and review of all the existing data respecting fossil invertebrates, endeavoring to depict their origins, developments, relationships, and trends.

In his discussion of the corals, Neumayr found little difficulty in linking the Mesozoic and Tertiary forms with the modern representatives of the group, but he was forced to leave the tetracorals in a somewhat uncertain position; we can perhaps do no better than consider his own words in this regard:

"Let us cast a backward glance over the entire field of the tetracorals which are provided with endothecal structures, and we thus find that the *Cyathophyllidae* form the mid-point, about which all the other families, the *Zaphrentidae*, *Axophyllidae*, *Cystiphyllidae*, and *Calceolidae*, group themselves; while, however, the three last named groups certainly represent strongly differentiated, diverging types, their significantly developed bilaterality makes it probable that the *Zaphrentidae* belong in another position, and show an original structure. *Streptelasma*, in particular, is a form which has been supposed to be the most primitive of the tetracorals known up to the present—an interpretation which is in complete accord with the geologic occurrence of this genus.

"In general, however, our knowledge in this regard is still fairly small, and the tetracoral branch could be put forth from the genealogical tree only with great difficulty, were it not for the remarkable phenomenon that the morphological relationships show a simple, straight line relationship, and not a network of offshoots. In other words, the existing relationships stand in good accord with the requirements of the theory of evolution, and the geologic sequence agrees with the accepted evolution in its general features." (1869, writer's translation, p. 270).

Neumayr believed that the bilaterality and peculiar mode of septal insertion of the tetracorals formed at once their most distinctive characteristic and the most promising clue to their future linkage with other groups.

As an important successor to James Hall in extending the knowledge of North American fossil corals there must be mentioned Amos Worthen, state geologist of Illinois. Like those of Hall, Worthen's labors were mainly confined to the description of new species, his material, however, being drawn from the Mississippian strata of Illinois and the adjacent states. (1889).

A descriptive work of much greater scope is that of P. Pocta, whose treatise on the Silurian corals of Bohemia appeared in 1894, as part of Barrande's "Systeme Silurienne du Centre de la Boheme." Pocta's work is of importance as a reference for the description and figures of a multitude of forms, but he confined himself for the most part to bare description of the external characters of his material.

Phylogeny of Haeckel

In 1896 Ernst Haeckel published the second volume of his "Systematische Phylogenie," As its title indicates, the purpose of the work is two-fold: the systematic classification of living and fossil forms on a morphological basis; and the synthesizing of both into a smoothly branching genealogical tree. Haeckel's attempt is more ambitious than the somewhat similar one of Neumayr, in that the latter confined himself to fossil forms only; and at first glance Haeckel seems to have been much more successful in achieving a connected evolutionary series. To do this, however, he was forced to postulate a considerable number of ancestral and linking groups which have no

known existence other than in the mind of the author. He justified the employment of such groups, however, by asserting that the morphology of known forms necessarily implied the existence of the postulated ones.

The order *Staurocorallia,* with its subdivisions, which Haeckel postulated to complete the evolutionary series of the corals, is typical of his use of hypothetical groups. As the ancestral type of the coral stock, Haeckel imagined a bilaterally symmetrical form exhibiting a fourfold arrangement; one having four tentacles, four major septa, and four visceral loculi. From such an ancient form he believed the later corals with six-fold, eight-fold, or higher symmetries to have been derived.

As a transitional group between the *Tetracoralla* and the *Hexacoralla,* Haeckel selected the *Mesocoralla,* or *Octozoantha,* forms whose tentacles and septa occur in groups of eight, or multiples of eight. The transition he conceived to have taken place through a doubling of the fourfold groups of the tetracorals to produce the eightfold type characteristic of the Mesocorals, and these in turn achieve the twelve septa and tentacles of the Hexacorals by the addition of four lateral ones. In support of this argument he called attention to the ontogeny of the hexacorals, which in the course of their early development go through a stage exactly recapitulating the eightfold symmetry of the members of the Mesocoral family *Edwardsia,* and then later add four more septa to achieve the typical hexacoral structure. In this ontogenetic development of the hexacorals, Haeckel sees proof of their Mesocoral ancestry. The close relationship of the former to the tetracorals, however, lacks any such concrete evidence.

Two other works appearing in the year 1896 warrant mention as important repositories of data on the genera and species of new areas. These are Lindström's description of the upper Silurian corals of the island of Gothland, and A. Stuckenburg's report on the Carboniferous corals of the Ural and Timan regions of Russia. The former is a model of careful analysis and description, with some attempts to place the forms studied phylogenetically. The latter is a much more general description of the coral fauna of a region hitherto almost unknown, and brings to light 136 new species of tetracorals and tabulates.

Morphology of Marie Ogilvie

In 1897 Marie Ogilvie, a student of von Zittel, attempted a most ambitious revision of the entire order Madreporaria. (1897a). The foundation of her work is a detailed microscopic study of the skeleton, analyzing the mode of growth, the relationships, and the evolutionary history of the component parts.

Miss Ogilvie found the Madreporarian skeleton to be built up of successive calcareous growth laminae, similar to those of mollusc shells. The fundamental unit of structure is the *caliculoblast,* an ectodermal cell in which, by a process of chemical change, lime is secreted and at once laid down within the cell in the form of aragonite fibres. Each lamina is alternately banded with a narrow zone, dark by transmitted light, and a broader, lighter, crystalline band. The former represent the proximal organic ends of the cali-

culoblasta, and the latter the fibrous deposits of the adjacent cells. These bands are less readily distinguished in progressively older forms.

After an exhaustive examination of the skeletal structures of representative genera of each living coral family, Miss Gordon attempted to trace peculiarities of structure backward through the genera of fossils, and to isolate phylogenetic groups on the basis of structural homologies and differences. She concluded that the evolution of the Madreporaria has proceeded without interruption from Paelozoic to modern forms, the transition from ancient to recent types taking place most pronouncedly in the Triassic and Jurassic periods. The many branches of the living Madreporaria spring mainly from two trunks, the *Madreporaria Haplophracta (Zaphrentoidea),* and the *Madreporaria Pollophracta (Cyathophylloidea.)* The one is characterized as a primitive group, slow to advance, and prone to retrogress, while the other has always been in the forefront of evolutionary advance, quick to adapt, and seldom retrograde.

In some contrast to Miss Ogilvie's work is the grouping of the corals put forth by W. Volz as a conclusion to his description of the corals of the St. Cassian strata, in 1897. Volz' classification attempts to be both historical and phylogenetic. He divides the corals into four groups:

I. The *Archeocyathidae* of the cambrian.

II. A Silurian and Devonian division, characterized by the families *Operculata, Cyathophyllidae, Cyathaxonidae, Paleocyclidae* and *Cystiphyllidae;* and a Carboniferous and Permian division in which most of the preceding genera show a pinnate septal arrangement.

III. A transition group introduced at the close of the Paleozoic, and marked by a mixing of ancient and modern forms. The *Styllophyllidae* and *Pinnacophyllidae,* both belonging to the Zaphrentoid stem, are most characteristic of this division. Of even greater significance for the evolution of later forms is the splitting of the *Cyathophyllidae* into the *Astraeidae* and *Thamnastraidae,* which is completed at the beginning of this period.

IV. The last evolutionary division of the corals is introduced during the middle Lias, and is characterized by a dominating trend in the direction of modern forms. At the outset of this group the *Astraeidae* and *Thamnastraeidae* are its most numerous forms.

Early Work of Weissermel

Yet another addition to phylogenetic theory was made in 1897 by W. Weissermel, in connection with his studies on the genus *Columnaria.* His ideas on the evolutionary stock of the corals may be readily interpreted from figure 5.

Weissermel also offered a suggestion as to the origin of the bilateral symmetry of solitary tetracorals. Postulating the existence of the coral cup on the sea bottom under conditions in which nutritive material was brought within range of the tentacles by a current streaming in a definite direction, he concluded that the polyp would tend to bend in the direction of the current, in order to present the greatest tentacular and oral area toward the supply of

food. From this would arise the characteristic cornute shape of the tetracoral corallum, and further, by virtue of its more favorable situation, the upper half of the calyx would tend to receive more nourishment than the lower, and in consequence would grow more rapidly and extensively. The bilateral symmetry of the tetracorals would thus be a consequence of this differential growth of the upper half of the calyx.

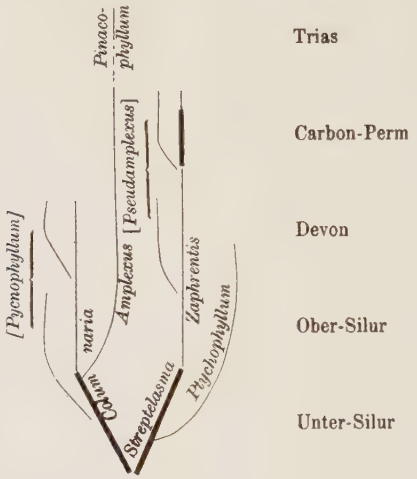

Fig. 5. Phylogeny of the Tetracorals according to Weissermel.

Structural Units of G. C. Bourne

The conception of the caliculoblast cell as the elemental structural unit of the coralline skeleton, an idea originating with von Heider, and elaborated by Miss Ogilvie, was strongly criticized by G. C. Bourne in a paper dealing with the structure of the Anthozoan skeleton, published in 1899. After a study of spicule formation in the *Alcyonaria*, and of the skeleton in *Heliopora* and a number of *Madreporaria*, Bourne concluded, as had von Koch, that the basic unit of the Anthozoan skeleton is a minute nodule or spheroid of calcium carbonate. These calcareous particles, according to Bourne, crystallize out of an organic liquid matrix secreted by the caliculoblast layer, and attach themselves to the pre-existing crystalline structures in such a way as to preserve the shape and orientation of the latter, exactly as in the growth of a crystal. The entire process of skeletal formation is analogous to the development of a crystal, and subject to the same laws, but in some manner, as yet unexplained, the general arrangement of the fasciculi of crystals is dominated by the living tissues which clothe the corallum.

Ontogeny of J. E. Duerden

Almost since the inception of their study, the primitive tetrameral symmetry of the *Rugosa* had been accepted as practically self-evident by the ma-

jority of workers, and this idea appeared to be abundantly confirmed by the discoveries of Kunth. The only noteworthy exceptions to this view were those of Ludwig and Pourtales, each of whom claimed to have observed six initial septa in the very earliest stages of certain tetracorals. The theory of a fundamental and primitive hexameral symmetry in Paleozoic corals was strongly championed by J. E. Duerden, in an extensive series of papers dating from 1900. As a result of grinding down the tips of a number of individuals of *Lophophyllum proliferum*, and examining the structure thus revealed in the earliest formed portion of the corallum, Duerden was able to confirm Pourtales' observation that this coral has six primary septa (protosepta), situated equal distances apart, and that new septa were added bilaterally in four of the six primary interseptal chambers, that is, in the two middle and the two ventro-lateral chambers. He observed further that the addition of new septa took place at only one region within each chamber—"immediately dorsal to the alar or vetro-lateral septum in the case of the middle chambers, and immediately next to the cardinal or ventral directive septum in the ventro-lateral chambers." (1906, p. 227).

By comparing the septa of fossil corals with the mesenteries of living ones, Duerden concluded that the *Zoantheae* are the closest living relatives of the *Rugosa*, for in the former the secondary mesenteries (metacnemes) are added bilaterally at one region within each of the primary ventro-lateral intermesenterial chambers, exactly as are the septa in the tetracorals.

From a study of the structure and development of the fossula in *Streptelasma rectum* Duerden derived further evidence favoring his theory that the *Zoantheae* and the *Rugosa* are closely related. He observed that the fossula in *Streptelasma rectum* is made up of a series of incomplete septa on either side of the cardinal septum, which is itself smaller than the other primary septa. This suggested to him that the atrophication of the cardinal septum could be correlated with the presence of a ventral gonidial groove similar to that of modern zoanthids.

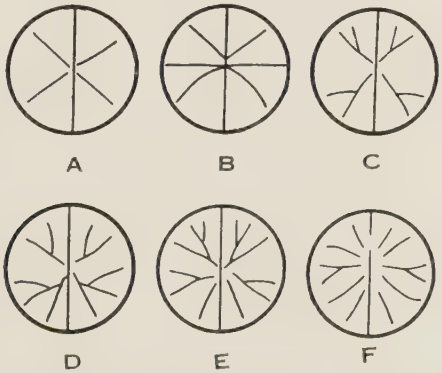

Fig. 6. Schematic representation of the insertion of the primary septa in *Lophophyllum proliferum*. (After Duerden)

Very shortly after its complete formulation, Duerden's theory was strongly criticized by C. E. Gordon, who affirmed that he had studied five or six young specimens of *Lophophyllum proliferum*, and in every case had found four primary septa extending farther into the tip than any other septa. Gordon explained the appearance of six primary septa observed by Duerden as being probably due to septal acceleration, whereby a pair of secondary septa, through premature development, simulated primary septa. (1906).

To this criticism Duerden replied at once, not only re-affirming his original conclusions, but listing four additional species in which he claimed to have discovered unmistakeable evidence of six primary septa. These species were *Cyathaxonia cynodon, Streptelasma rectum, Zaphrentis pusilla,* and *Duncanella borealis,* and for each of them he published serial sections evidencing a hexameral symmetry in the initial stages of development. (1906b).

Morphological Theories of H. M. Bernard

During the period in which Duerden was thus engaged in developing his theory of a hexameral ancestry for the tetracorals, H. M. Bernard, of England, offered some entirely new concepts of the synthesis of the Madreporarian skeleton. Bernard centered his study around the "prototheca," a tiny saucer-shaped structure which he conceived to be the first step in the development of an individual skeleton or the parent calicle of a colony. According to his definition,

> "This *prototheca* is not a composite structure, but a morphological unit, the rim of which can be bent up, flattened completely down, and indefinitely expanded in any direction as a film, from the upper surface of which, as originally from within the cup, the coral skeleton arises. . . This film is the Epitheca." (1904, p. 4).

In thus concluding the epitheca as part of the prototheca, Bernard differs from von Koch's conception of the "basal plate," since the latter considered the epitheca an independent structure, and described it as the "outer plate."

In the successive formation of protothecid saucers, and their epithecal phases, Bernard felt that he had an important clue to the structure of corals, and he summarized his theory as follows:

> "For an understanding of the morphology of the coral skeleton, we must bear in mind that essentially the same process, viz., *a succession of epithecal cups or saucers, occurs throughout the whole of the Madreporaria.* They may be simple conical cups, fitted one into the other *(Zaphrentis)* or flat plates piled up *(Montlivaltia, Goniopora)*, or their epithecal floors may be thrown into complicated folds and both the cup and its repetitions may be difficult to unravel, but the fundamental principle is the same throughout. . . . We repeat then, for the sake of emphasis, that wherever the epitheca occurs it represents the rim, or the coalesced rims, of one or more protothecal cups or saucers, the floors of which are represented by the tabulae. In any individual case the tabula below the living layer is the *n*th repetition of the original prototheca of the parent polyp." (1904, p. 9).

As a supplement to the foregoing theory, Bernard also attempted to explain the shape of the adult corallum in terms of the prototheca. He suggested that cornute solitary corals, such as *Zaphrentis* and *Menophyllum*, owe their horn shape to the falling over of the prototheca, with its gravitative effect on the tissues instituting the septa, later growth into a vertical position

once more giving rise to a secondary radiality. Bernard considered the entire group *Tetracoralla* to be no true division of the corals, but merely an assemblage of forms whose common characteristics of shape and structure were derived from this early falling-over of the prototheca.

In the belief that the shape of the prototheca is a character of diagnostic importance, Bernard devised methods for diagraming it, and attempted to employ such diagrams in tracing phylogenetic relationships. Some idea of his prototheeal types, and the manner in which they are combined to produce varied forms of coralla, is given in figure 7.

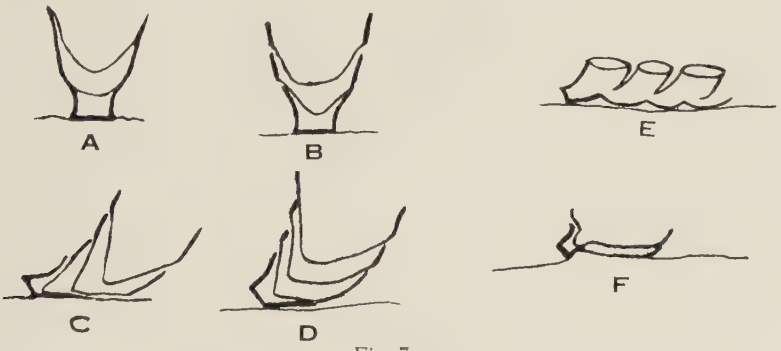

Fig. 7.

a) The three earliest growth periods of a primitive Madreporarian. The thick basal part is the prototheca.
b) Same, regarded hypothetically as three separate cups. (The lowest is the prototheca.)
c) Early stage like (a), but having fallen over and begun upright grow again. Fossula on the convex side.
d) Falling over of a wide-mouthed prototheca. Fossula on the convex side.
e) Method of budding of prone prototheca.
f) One sided bending over of prototheca. (After Bernard).

Ontogenetic Studies of Carruthers

The theory that the *Rugosa* possess six primary septa received strong additional support in a paper published in 1906 by R. G. Carruthers. (1906). For the purpose of definitely settling this much disputed point, Carruthers sectioned the tips of a variety of tetracorals, chiefly Zaphrentids, and worked out the plan of their septal insertion in careful detail. The various stages of the development of the septa, as he observed them, are as follows:

I. A single septum stretches entirely across the calicle, from wall to wall. At a considerably later stage this breaks near the center, the two halves forming the cardinal and counter septa. This first formed septum Carruthers designated as the "axial septum."

II. Two new septa arise, one on either side of the axial septum, at its cardinal end. These remain attached to the wall of the corallum and to the

axial septum, but gradually spread outwards, and eventually become the alar septa.

III. A second pair of septa appear at the counter end of the axial septum, and similarly spread outward, but to a much more limited extent than the first pair.

The disruption of the axial septum completes the formation of six primary septa. Secondary septa are likewise inserted in pairs, arising on the fossular surfaces of the last formed septa, but instead of moving outwards, as did the lateral primaries, they all move toward the counter septum. The entire plan can readily be understood from a study of the appended diagram.

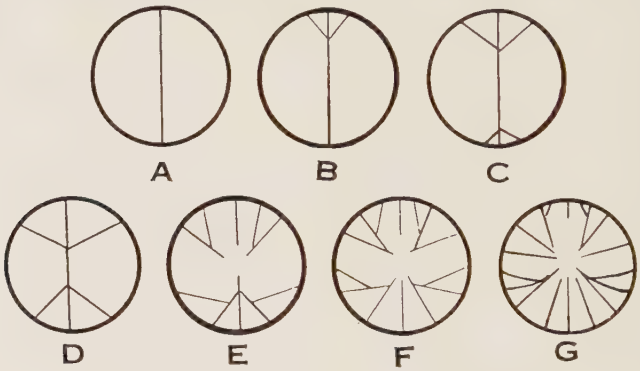

Fig. 8. Diagram showing the development of the protosepta in Tetracorals as observed by Carruthers.

The explanation of septal insertion offered by Carruthers was called into question by T. C. Brown, in a paper published in 1909. After a study of the early stages in the development of *Streptelasma*, a genus also analyzed by Carruthers, Brown found the structure to be exactly as Carruthers had represented, but he disagreed with Carruthers in the manner of interpreting it. Brown suggested that the two counter primaries could be better interpreted as secondary septa. He insisted that failure to so interpret them would involve the necessity of assuming for *Streptelasma* a septal arrangement entirely different from that of any other rugose coral, as the cardinal quadrants would then have one more pair of septa than the counter quadrants.

In 1909 L. Faurot, of France, published the results of his study of the septal development of *Cyathaxonia*, and essentially corroborated the scheme of septal insertion offered by Carruthers. Faurot found that the tetracorals, as represented by Cyathaxonids, have six primary septa, and he verified the existence of a single initial axial septum, as described by Carruthers. His diagram of the first stages of septal development in *Cyathaxonia* differs from the diagram of Carruthers only in minor details.

Faurot's primary purpose, however, was to compare the septal develop-

ment of the *Rugosa* with that of the Hexactinids, Zoanthids, and Cerianthids, to determine the degree of relationship existing between them. He concluded that the Cerianthids are the unique descendants of the tetracorals, for they alone among living corals preserve the primitive disposition of the septa into four groups. (1909a).

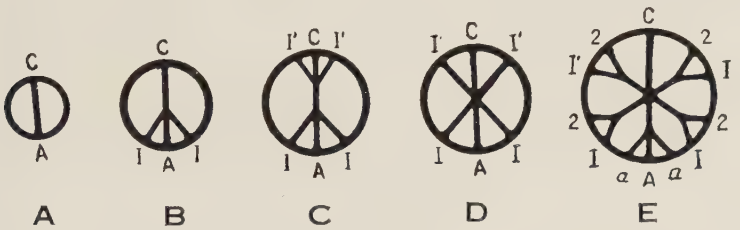

Fig. 9. The development of the protosepta in *Cyathaxonia.* (After Faurot)

An important step in unravelling the complications of the genus *Zaphrentis* was taken by Achille Salée in his revision of the genus, *Caninia,* published in 1910. Salée was able to determine a number of diagnostic characters separating *Zaphrentis* from *Caninia,* and he also simplified taxonomy by showing that the forms described by Milne-Edwards and Haime, and de Koninck, as *Zaphrentis vermicularis, Z. Dumonti, Z. Nystiana, Z. Edwardsiana,* and *Z. cornu-bovis* are actually only successive stages in the development of *Caninia cornucopiae.*

Morphological Theories of Yakowlew

For more than a decade subsequent to 1910, N. N. Yakowlew, of Russia, devoted a series of papers in three languages to an effort to elucidate the origin of the structural peculiarities characterizing the *Rugosa.* As important differences between the *Rugosa* and the *Hexacoralla,* he cited the conical polyparium of the former, as contrasted with the cylindrical one of the latter, and the lateral attachment of the tetracorals, as opposed to the tip attachment of the hexacorals. The habit of lateral attachment evinced by the tetracorals Yakowlew suggested might be correlated with their life in shallow epicontinental waters, subject to agitation from strong currents and large waves; the hexacorals, dwelling in greater depths, had less need for rigid support. Like Weissermel, Yakowlew explained the cornute shape of the tetracoral polyparium as being due to orientation with respect to the prevailing currents, but he exactly opposed Weissermel by holding that the bending was away from the current, to avoid suffocation from sediments, and not toward it to obtain food. (1917a).

With regard to the internal structure of the coral skeleton, Yakowlew believed that the insertion of secondary septa was a function of the conditions imposed by the curved state of the corallum, and the mechanical difficulties entailed by the pre-existence of the primary septa. He observed further that the mouth of a conical polyparium is commonly in a plane perpendicular to the convex side, and that the secondary septa have a tendency to grow in a

plane perepndicular to that of the mouth. The outcome of these conditions is that it is possible for the secondary septa to grow unimpeded, in the manner stated, only in the two counter quadrants. In the cardinal quadrants they are forced to grow in such manner that their outcrops on the wall of the corallum are parallel with those of the alar septa. This structure and its possible variations are shown diagrammatically in figure 10. (1915).

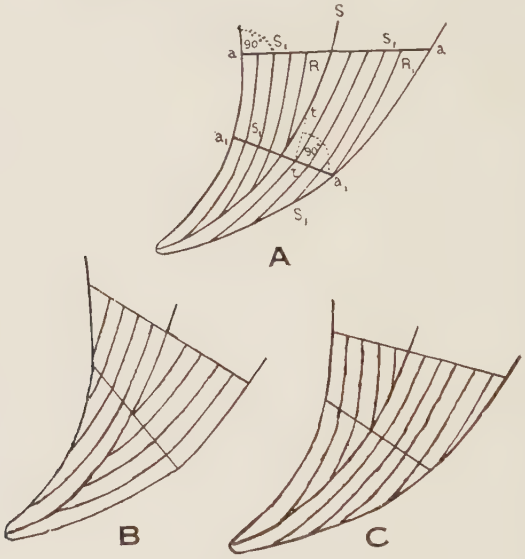

Fig. 10. Diagram showing the outcrops of the septa on the surface of the polyparium, according to whether the mouth is at right angles to the concave side (a), to the convex side (b), or to neither (c).

A good summary of the evidence bearing upon the ancestry of the hexacorals, and their possible relationship to the tetracorals is presented by J. W. Robinson in a paper published in 1917. After considering the alternative possibilities that the *Hexacoralla* are either directly descended from the *Tetracoralla,* or that they existed through the entire Paleozoic as soft-bodied, skeletonless forms, Robinson concludes in favor of the former theory. The principal factor influencing his conclusions is the widespread development of a columella among the tetracorals toward the close of the Paleozoic, for this structure is also found extensively developed among the hexacorals at their inception in the Mesozoic.

The theories of Yakowlew regarding the influence of sessility and lateral attachment in determining the shape of the tetracoral polyparium were seconded by Otto Jaekel in a paper published in 1918. Jaekel, however, felt that it was necessary to consider a still earlier stage of coral ontogeny than had Yakowlew, and to explain those feautres in the structure of a coral which are present at its inception as an individual, and which antedate any possible influence of environment. For this purpose he employed the *Planula* larva of

the *Anthozoa,* a free-swimming, worm-like form. He suggested that at the close of its larval existence, the *Planula* folded upon itself like a U-tube, so as to bring its oral and posterior ends into conjunction, the extremities and ventral surfaces fusing together. This form, he suggested, might represent the initial stage in the existence of a coral, the subsequent structural developments being controlled by the peculiarities of the two halves of the larva. As the principal evidence in favor of his hypothesis, Jaekel pointed out that the corallum of a tetracoral was naturally divided into two unequal and dissimilar portions by a plane passing through the Alar septa. In one such area the septa were inserted in a pinnate fashion, while in the other a radial arrangement prevailed. These differences, according to Jaekel, are to be correlated with the origin of the two areas from the posterior and anterior halves of the larval form, the Alar septa being the reflection of the ventral fusion.

Although of relatively minor scope, it is of some technical importance to note that in keeping with the foregoing work, Jaekel corrected a misconception regarding the position of the *Rugae* or stripes seen upon the external surface of the corallum in a wide variety of tetracoral genera. He showed that these rugae were not continuous in position with the septa, but represented rather the position of the tentacles, and were consequently the external reflection of the interseptal loculi. From this he made it apparent that the Cardinal septum, situated in a fossula composed of two such loculi, will be represented on the external surface of the corallum by two parallel rugae.

Shortly after Jaekel published his theory of Anthozoan structure, A. Krempf, in a report to the Academy of Sciences in Paris, announced that a study of Anthozoan embryos had yielded him unmistakeable evidence of a primitive bilateral symmetry, present in the embryo in the very first hours of its existence, and in this respect differentiating the *Anthozoa* from all other *Cnidaria.* (1919, 1919a).

Theories of W. D. Lang

In 1917 and 1923 W. D. Lang, of England, published two very important discussions dealing with the influence of homeomorphy on the classification of corals, and setting forth the dominant trends which seem to have governed coral evolution. Lang cautioned against too readily refering to the same lineage forms separated by great chronological intervals, even though they appear to show conspicuous similarities of structure. In support of this warning he cited the well known fact that similarity of environment and function tends to bring about similarity of structure. As possible examples of such convergence he suggested the ancient *Heliolites* and the modern *Heliopora,* which are commonly considered to stand in direct genetic relationship to each other, and pointed out that if they are truly of the same lineage, it is strange that not one of the intermediate forms has been preserved in the geological record. A similar condition exists between the ancient *Syringopora* and the modern *Tubipora,* and among numerous other forms.

Of the greatest importance to the formation of homeomorphs in corals, however, Lang considered the existence of certain definite lines of evolution which are persistent in their expression. He defines four such evolutionary

tendencies: (1) Failure to part with the products of fission and budding; such, for example, as produces a *Thecosmilia* from a compound *Montlivaltia*. (2) Increased extension of the corallum resulting from incomplete fission at the distal end, giving meandriform corals. *(Latimeandra. Phyllogyra, Meandrina)*. (3) Communication of the corallites through abolishing separating walls, producing coralla of individuals with confluent septa. *(Thamnastria)*. (4) Perforation of the corallites, resulting in a reduction of the skeleton through the medium of pores. From this arise the numerous modern genera known as the "perforates," such, for example, as *Porites* and *Goniopora*. Fossil examples are *Kobya* and *Microsmilia*. More than any other factors, the expresion of these four tendencies are responsible for the formation of homeomorphs, and efforts to relate the *Tetracoralla* and *Hexacoralla* are apt to be based on homeomorphy rather than true descent. Lang favored the idea that the tetracorals died out at the close of the Paleozoic period, and were replaced by the hexacorals, which arose anew from a soft-bodied ancestor.

After having emphasized the difficulty of recognizing characters which are truly diagnostic of coral genera, Lang attempted the solution of this problem in its application to Carboniferous corals by classifying them in accordance with the type of "trend" which appeared to have governed their development. His discussion is begun with a consideration of the various types of corallum, which he classifies as follows: (1) Haploid –a simple cornute form; (2) Dendroid—a finger-like aggregate of cups; (3) Phaceloid—a bundle of corallites lying approximately parallel; when these are so closely packed together as to become polygonal, they are (4) Cerioid; when the boundaries of the Cerioid forms become indefinite they are (5) Astraeoid; and when the septa of contiguous corallites become confluent, the corallites are (6) Thamnastraeoid.

Lang then makes a survey of the Carboniferous corals, and defines the following trends:

1. *Astraeoid trend*—an evolutionary tendency directed toward the achievement of the Astraeform type of corallite.

2. *Caninoid trend*—a trend in the shape of a single corallite from discoid through trochoid to cylindroid.

3. *Cyathophylloid trend*—a tendency to radial symmetry, with obscuration of the bilateral symmetry through the introduction of secondary septa, reduction of the Cardinal septum, and arrangement of the septa in groups of four.

4. *Amplexoid trend*—evidenced by the distal retreat of the septa.

5. *Lonsdaleoid trend*—evidenced through a proximal retreat of the septa.

6. *Cystiphylloid trend*—shown in the development of dissepiments.

7. *Aulophylloid trend*—a trend toward complexity and irregularity of the central column.

8. *Petraeoid trend*—a secondary thickening through the filling in of space caused by the distal retreat of the septa.

Through the application of the foregoing criteria, Lang was able to divide

the Carboniferous corals into groups which he considered to be truly related genetically. Figure 11 shows typical cross-sections of representative members of each of these groups.

Gerth

In 1919 H. Gerth offered further evidence tending to confirm an initial six-fold symmetry in tetracorals. In a paper devoted to a review of the development of the septal apparatus in ancient and modern corals, Gerth figured thin sections of *Plerophyllum radiciforme,* from the Permian of Timor, which showed both the first and second pairs of Alar septa strongly developed over the Metasepta. The visible existence of a second pair of Alar septa, thus afforded, strongly verifies the six-fold plan of septal development urged by Duerdin and Carruthers. Gerth also pointed out that the succession in the appearance of the first six mesenteries in the young of modern corals is analogous to that of the primary septa of the *Rugosa.* All further septal and mesentery formation in recent corals is as a rule cyclic, and later insertion in certain positions and repression of new structures in others is a consequence of asymmetrical growth of the calyx. Similarly, the metasepta of the *Rugosa* are inserted in four of the six primary interspaces as a consequence of repression and asymmetric growth. Gerth contended that there was no profound structural difference prohibiting a direct relationship between the *Rugosa* and living *Madreporaria.*

Phylogeny of F. W. Sardeson

A unique viewpoint regarding the ancestry of the corals is that published in 1924 by F. W. Sardeson. This writer regards Ordovician corals of the genus *Tetradium* as ancestral to both tetracorals and tabulates. He attempts to show diagrammatically that differential retardation of cell fission in *Tetradium* is the logical preliminary to the formation of the two distinct types of cell found in *Heliolites,* which is thus considered a descendant of *Tetradium.* On the other hand, if the retardation of cell fission in *Tetradium is* carried to the extreme, a form similar to *Streptelasma* may be produced. Sardeson also suggests that Tetradium may be related to the sponges by way of the *Archeocyathids.* The evidence adduced, however, scarcely seems to support the magnitude of his conclusions.

Weissermel

A very fine survey of the similarities and differences of the tetracorals and hexacorals, with a view of deducing their relationships, was given in 1927 by W. Weissermel. In contrasting the two groups, Weissermel emphasized the following points: (1) The tetracorals possess four conspicuous primary septa; the hexacorals have six. (2) Septal insertion in the tetracorals is definitely localized, but in the hexacorals new septa are added over the entire periphery. (3) The tetracorals develop only two cycles of septa, whereas the hexacorals commonly have more than two, although some forms are known which possess septa of only the first and second orders. (4) The hexacorals commonly expand by lateral growth; the general direction of growth of the

tetracorals is upward. (5) The tetracorals almost always have a well developed theca, but among the hexacorals this structure is frequently lacking or much reduced. (6) The tetracorals have the rugae opposite the interseptal spaces; in the hexacorals the rugae are analogous to the septa themselves. (7) A coenenchyma is common among the hexacorals, but it is scarcely known among the tetracorals. (8) The columella is of uncertain significance, but a pseudo-columella is much more common in the tetracorals. (9) The hexacorals have a strong tendency to develop a porous skeleton, a condition rare in tetracorals. (10) The development of synapticulae to support elongated septa is peculiar to the hexacorals. (11) The tetracorals have a tendency to an elongated, tube-like shape, which, when duplicated by the hexacorals, gives rise to form analogous to the tetracorals, as is shown in the tabulae and disseppiments, and the lack of synapticulae exhibited by the *Astraeidae*.

Weissermel suggested that the tabulates arose from the extreme constriction of the calicular diameter caused by energetic vertical growth. The other characteristic tabulate features, such as reduction of septa and strong development of tabulae, follow naturally from such a condition. When a marked reduction of the calicular radius occurs in the hexacorals, the resulting forms are very similar to the tabulates. *(Alveopora, Favositipora, Heliopora)*.

After considering the evidence for six Protosepta in the tetracorals, Weissermel concludes in favor of such a condition, and then proceeds to the description of the transition group of forms showing a mixture of both tetracoral and hexacoral characteristics. Foremost among these is the genus *Plerophyllum*, from the Permo-Carboniferous of Australia and Timor, in which there are five well developed Protosepta. Gerth observed that the insertion of septa in *Plerophyllum* was after the orthodox tetracoral fashion except for the development of the third pair of Protosepta. A second transitional form is *Polycoelia profundum*, which displays a disposition to develop more than two cycles of septa, and to suppress the bilateral arrangement. In *Prosmilia cyathophylloides* and *P. angusta* there are five distinct orders of septa. *Pinnacophyllum* and *Omphalophyllia* are Permian genera which have almost lost the differentiation between protosepta and metsepta.

Fig. 11.

A-F Transverse Sections of Carboniferous Corals.
a. *Zaphrentis*
b. *Palaeosmilia*.
c. *Lithostrotion*.
d. *Lonsdaleia*.
e. *Amplexus*.
f. *Caninia* (typical form).

G-I Sections of Central Columns of Clisiophyllid Corals.
g. *Clisiophyllum*.
h. *Rhodophyllum*.
i. *Aulophyllum*.

J-L Sections of Carboniferous Corals.
j. *Caninia* (advanced stage).
k. *Cyathaxonia*.
l. *Carruthersella*.

(After W. D. Lang)

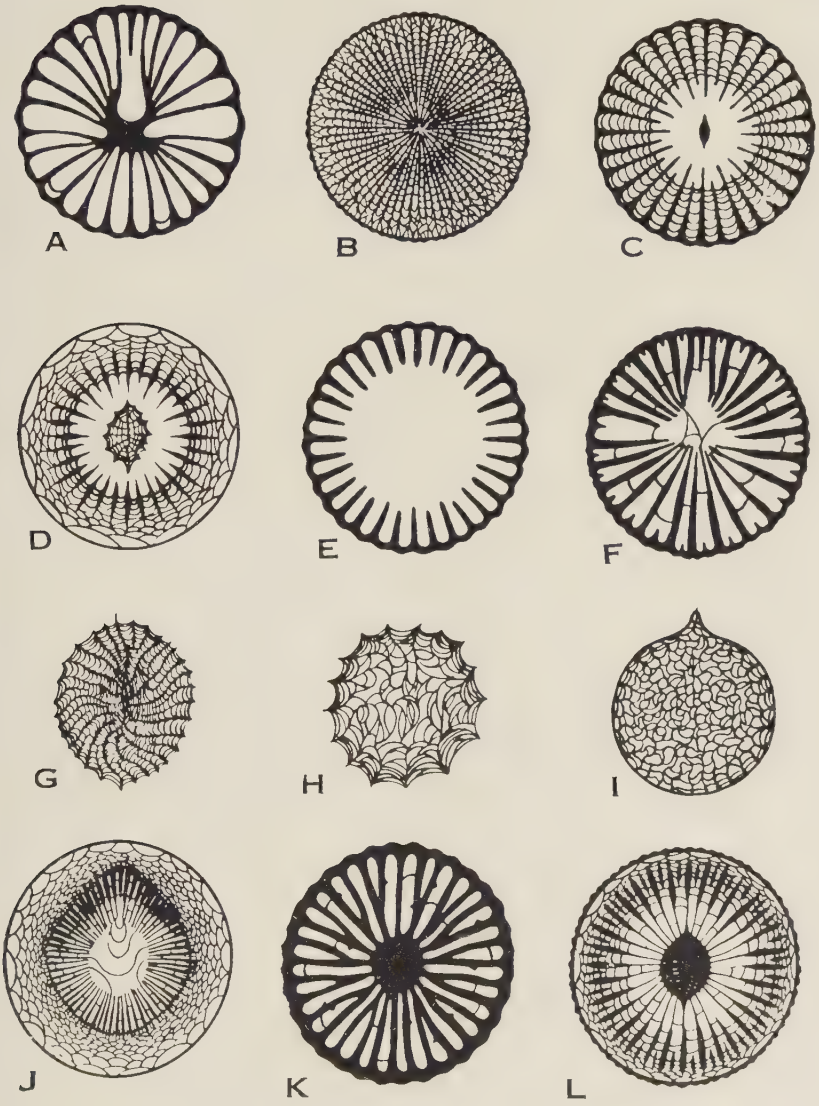

Fig. 11

From this comparison of tetracorals and hexacorals, and from the characteristics of the intermediate genera, Weissermel concluded that the hexacorals are the direct descendants of the tetracorals, the propagation taking place through a very limited number of genera which by virtue of their favorable location were able to survive the rigorous conditions of the Permian.

Weissermel's views have since been strongly supported by Otto Schindewolf, who has carried further the studies on Permian forms. (1930, 1930a, 1931). From an analysis of the literature, and from his own studies on the tips of the Paleozoic corals, Schindewolf finds good evidence for attributing a primary bilaterality to the tetracorals. He contends that the bilateral disposition of the septa is primitive, and the later pseudo-radiality is the result of environmental conditioning, being especially the result of a sessile habit.

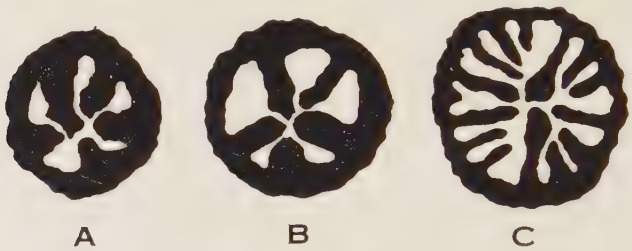

Fig. 12. Youthful stages in *Plerophyllum timorense* (Gerth) (After Schindewolf.)

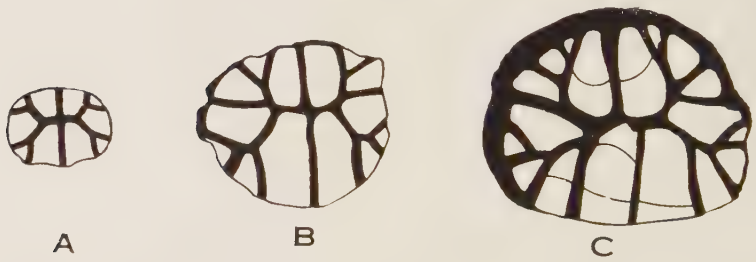

Fig. 13. Early stages in the development of *Hapsiphyllum konincki*, (Edw. & H.) (After Schindewolf).

Richter's Study of the Operculates

The study of the operculated corals, which had already been carried to a high stage by Lindström, received a further important contribution through the researches published in 1929 by Rudolph Richter. Considering first the origin of the plano-convex form and the remarkably parallel growth lines of *Calceola, Richter* endeavored to show that these are but natural consequences of the possession of an articulated operculum. He contended that a broad, even edge is a mechanical necessity for the production of a satisfactory joint,

and once this is achieved, the flattened side and parallel strippings result merely from continued growth, and are not functional. There will thus be as many flattened sides as there are opercula, the number varying from one, in *Calceola,* to four, in *Goniophyllum.*

Richter agreed with Lindström in holding that whereas the calyx of the operculates is homologous with the calyx of other tetracorals, the operculum is an entirely new structure, and is not duplicated in the remainder of the *Rugosa.*

Conclusion

If, from the preceding summary, we endeavor to seek out those data which seem firmly established, and may thus be employed as tools for the future analysis of corals, we find that there is still relatively little which is beyond the pale of controversy.

Evidence is steadily accruing in favor of the initial hexameral character of the tetracorals, and concomitantly favoring the phylogenetic relationship of the tetracorals and the hexacorals. The factors inducing a suppression of the counter quadrants in the tetracorals, and thus producing a secondary tetrameral symmetry, are still uncertain, but seem assignable to mechanical changes arising from environmental adjustments. The ontogeny of corals is yet a relatively unexplored field, whose possibilities are only emphasized by the works of Duerden, Carruthers, and Salée.

In the study of the corallum itself we are on firmer ground, but here too there is a wealth of uncertainty. The secretion of the calcareous material of the skeleton has been given diverse interpretation by Lacaze-Duthiers, Ogilvie, and Bourne. The fossula has been described in turn as a gonidial groove, a mechanical consequence of sagging tissues, and an outlet canal for food bearing currents. Even such apparently simple apparati as the tabulae are susceptible to a broad range of explanations, as witness Bernard's concept of protothecae; and the function of such specialized appliances as the columella is almost wholly unknown.

On the other hand, the study of the septa has been carried to a high stage of perfection by Pratz, von Heider, and Ogilvie, and the nature of septal insertion has been clearly delineated. Von Koch has similarly done excellent work on the study of the theca, and his researches, together with those of Nicholson and Studer, have combined to give us a full understanding of asexual reproductive forms.

In the field of technique modern students have made marked strides, and the employment of grinding or slicing to produce serial sections, together with the improvements in the use of the camera and camera lucida as means of depiction, is the foundation of all our progress in the paleontology of corals.

It is in the classification of corals that we find the least advance has been made. This event, however, is to be expected, since progress in classification is dependent upon progress in all other branches of study. The systematizations of Milne-Edwards and Haime, or of Zittel, are still the authoritative

ones to-day. Perhaps the most marked suggestion of progress is W. D. Lang's proposal of "trends" as a means of grouping, but this is far from being a formal classification, and is at best but a re-vamping of the concept of type genera urged by Thomson and Nicholson. We are still far removed from a natural classification of the corals, based upon true kinship rather than upon chance resemblance of form, but the growing mass of data on ontogeny and homeomorphy seems to assure us of eventually achieving this end.

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STUDIES IN PALEOZOIC CORALS

III.—A Revision of Some Mississippian Zaphrentids*

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A.—Introduction

The existing classification of the tetracorals of the Mississippian period in North America has resulted largely from the accumulation of numerous isolated descriptions of species, collected from a wide area, and delineated sporadically through a considerable period of time. With the progressive depletion of the number of obviously new forms has come a waning of interest, and the Mississippian corals have been permitted to remain a group whose principal basis for unification has been their common occurrence in strata of essentially the same age.

It is a tribute to Milne-Edwards and Haime that the first extensive treatment of American Mississippian corals should be at the hands of these French authors. In their *Polypiers Fossiles des Terrains Palaeozoiques*, published in 1851, five genera and fourteen species of cup corals are described from the Mississippian of North America, and in 1860 Milne-Edwards redescribed all these and added four new species in volume three of his *Histoire Naturelle des Coralliaires*.

The common usage of the French treatises as reference texts has perhaps led most of the American workers who dealt with Mississippian corals to attempt to refer their species to genera contained therein, rather than to derive their taxonomy from a completely independent analysis of the material studied.

In the Twelfth Annual Report of the Hayden Survey, published in 1878, C. A. White described a number of Mississippian corals from Iowa and Missouri, thus supplementing the single species described from Iowa by James Hall in 1858.[1] White's dependence upon the work of Edwards and Haime as a guide to the determination of genera is shown both by his nomenclature and the manner in which his descriptions are modelled.[2] A similar tendency is manifest in the work of Amos Worthen, whose descriptions of corals from the Mississippian strata of Illinois and the adjacent states, published in 1890, is the first American work dealing with any considerable number of forms. The eighteen species described by Worthen are referred

* Parts I and II of these studies appeared in this journal, **15**, (2): 97-137, 1934.

1 Hall, J., Geol. Iowa, **1** (2): 650, pl. 22, 1858.

2 White, C. A. Cont. to Invert. Paleon., No. 8; 156, in 12th Ann. Rept. Hayden Survey, 1878.

to genera established by Milne-Edwards and Haime, sixteen species being placed in *Zaphrentis* alone.[3]

A year after the appearance of Worthen's work, S. A. Miller published a similar discussion of Mississippian corals from Missouri and Indiana. Here again we find that nine of the eleven species of tetracorals described are referred to the genera *Amplexus* and *Zaphrentis*, although Miller also created the genus *Cystelasma* and placed two species in it.[4]

In 1894 Charles R. Keyes, as state Geologist of Missouri, described the corals of that area. His discussion, however, amounts to little more than abstracts of the descriptions of previous writers. [5] The work of Miller in Indiana was continued during the years 1898 to 1906 by the analogous studies of Greene[6] and Beede.[7]

The first considerable step toward the independent derivation of a generic taxonomy from the study of American material is found in the generic revisions published in 1900 by George B. Simpson.[8]

This work resulted in the creation of 18 genera of Paleozoic corals based solely upon American species. At least five of these genera are directly applicable to Mississippian forms, notably, *Meniscophyllum*, *Hapsiphyllum*, *Triplophyllum*, *Schoenophyllum*, and *Homalophyllum*. The immediate consequence of Simpson's work has been the introduction of a dual terminology into the writings of later American paleontologists, some having elected to retain the original nomenclature, others having recognized Simpson's genera. This is especially true in regard to the genera *Hapsiphyllum*, *Triplophyllum*, and *Homalophyllum*, which were separated by Simpson from the genus *Zaphrentis*.

In 1914 Marjorie O'Connell published an analysis of the genus *Zaphrentis*, giving full support to the genera created from *Zaphrentis* by Simpson as well as a clear delineation of *Zaphrentis* itself.[9]

Recent years have seen many descriptions of Mississippian tetracorals from America, chiefly as members of local faunal lists, but no attempt has been made to unify the species under clearly depicted genera. Philosophical surveys of the relationships, occurrences, and trends of the Amrican forms have been even more conspicuously lacking.

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3 Worthen, A. H., Geology of Illinois, **8**: 71-82, 1890.

4 Miller, S. A., 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 616-623, 1892.

5 Keyes, C. R. Missouri State Geol. Surv., **4**: 104-124, 1895.

6 Greene, G. K., Contributions to Indiana Paleontology, **1**, pts. 1-20. 1898-1904.

7 Beede, J. W., 30th Ann. Rept. Indiana Dept. Geol. Nat. Res.; 1201-1218, 1905-1906.

8 Simpson, G. B., New York State Mus. Bull. **39**: 199-222, 1900.

9 O'Connell, M., Ann. Acad. Sci. New York, **23**: 177-92, 1913.

B. — Systematic

Class Anthozoa Gistl.

Order Tetraseptata Grabau

Sub-order Proteroseptata Grabau

Family *Zaphrentidae* M.—E. & H. (emend. Grabau)

Simple conical to cylindrical corals derived from the *Streptelasmaidae*, with the primitive types of which the early stages of the *Zaphrentidae* always agree. Septa quadripartite in the earlier stages, becoming more or less radial in the later; sometimes twisting at the center, in others (highly specialized types) assuming a breviseptal (amplexoid) character, i. e., falling short of the center. Fossula always well developed, in more specialized types becoming a siphono-fossula. Cardinal septum usually very short in the adult, or even almost completely aborted; the secondary septa on either side often retaining their pinnate arrangement, or bending towards each other. Carinae present in a few specialized types. Tabulae well developed in all but the primitive types where they may be wanting. Dissepiments generally well developed in the more typical genera. No columella, but a slight twisting of the septa in the center may suggest a streptocolumella. Range: from Silurian (?) to Carboniferous[10].

Genus *Triplophyllum* Simpson

Triplophyllum. Simpson, New York State Mus. Bull. **39**: 209, figs. 26-27, 1900.

Triplophyllum. Simpson, Univ. State New York, State Mus. Rept. 54, **3**: 209, figs. 26-27, 1902.

Tripliphyllum. O'Connell, Ann. New York Acad. Sci., **23**: 192, 1913.

Genotype.—Zaphrentis terebrata Hall, 12th Ann. Rept. Ind. Dept. Geol. Nat. Hist.: 316, 1883. Onondaga limestone, Falls of the Ohio.

Example.—Zaphrentis centralis Edwards and Haime, Mon. polyp. terr. pal.: 328, pl. 3, fig. 6.

Description.—In segregating the genus *Triplophyllum* from the genus *Zaphrentis*, Simpson characterized it as follows:

This genus has the same appearance and mode of growth as *Zaphrentis*, but in addition to the septal fovea there are two lateral foveae. The microscopic character is also different. In *Zaphrentis* the calcareous fibres of the septa are arranged obliquely outward from the median plate; in this genus they are arranged obliquely inward, or toward the center of the corallum.

Fig. 1. Diagramatic cross-sections of *Zaphrentis dalii* E. & H., to show the characters of *Triplophyllum*. After Simpson.

10 Chi. Y. S., Palaeontologica Sinica, B. **12** (5): 16, 1931.

Medium to large solitary corals. Corallum cornute, but varying from nearly straight to moderately curved, especially near the tip. Epitheca thin; always marked by pinnately arranged rugae and by growth annulations or swellings. Ornamentation by means of small spines is found in some species. Spines may be arranged in orderly rows, or scattered in an apparently random manner over the surface of the corallum. Calyx moderately broad and deep, but occupying less than one-third of the whole corallum. Septa in two cycles, primaries strong and well developed; secondary septa may be so rudimentary as to be practically obscured in the calicular view or may be formed so late in life as to be entirely confined to the free edge of the calyx. Primary septa reach the center of the calyx except where fused together to form the fossular wall. Fossula large and deep, extending from the margin to the center of the calyx; its position varies slightly, but is always on the concave side of the corallum. It is commonly smoothly walled by the lateral fusion of the adjacent counter-quadrant septa. Most members of this genus must have reproduced through sperms and ova, as examples of budding and fission are almost unknown.[11] Well defined scars of attachment are very rare in the majority of species.

Internal characters. The two alar fossulae diagnostic of this genus generally are best developed in the late neanic stages, although examples are common in which the alar fossulae are clearly perceptible in the calyx. With progressive maturity the increase in the number of septa brings about a pseudo-radiality which tends to obscure or even entirely eliminate the lateral fossulae. (Pl. 10, Figs. 1, 5; Pl. 11, Fig. 8). The cardinal fossula is large and firmly walled in all but nepionic stages. It is formed from the lateral fusion of the adjacent septa, the first pair of metasepta adjacent to the cardinal septum being especially important in bounding the cardinal fossula. The cardinal septum, which in the early stages is the largest and most prominent of the septa, is usually steadily recessive, and in full maturity is rudimentary. Secondary septa are not found before the ephebic stage, and frequently are inserted much later. Tabulae are well developed throughout the entire corallum, but dissepiments are relativly few in number, and are most abundant in the older portions of the corallum.

Remarks.—The oblique inward orientation of the calcareous fibers of the septa, cited by Simpson as a generic character of *Triplophyllum,* is of very doubtful value for purposes of identification. Such orientation can be reliably detected only in sections of petrographic thinness, and it is commonly entirely obliterated in silicified specimens.

The development of alar fossulae in the nepionic or early neanic stages of a tetracoral is a normal consequence of septal insertion in accordance with Kunth's laws, and is of widespread occurrence in Palaeozoic corals. A retardation of development which preserves the alar fossulae into the ephebic and later stages is, however, a specialization which may justly be considered of generic significance. In those Triplophyllid corals which are described in

11 White, C. A., On spontaneous fission (?) in *Zaphrentis.* Amer. J. Sci. (3) 5: 72. 1873.

the succeeding pages there is a marked variation in the extent to which the alar fossulae are preserved in the mature portions of the corallum. In each species, however, three fossulae are distinct at a late neanic or early ephebic stage, periods too late in the ontogeny to be the unmodified consequences of a common habit of septal insertion. In addition to their value as a generic index, the fossulae of *Triplophyllum* constitute a biocharacter upon which changes of palingenetic significance might readily be traced, and the genus possesses gentes suitable for such study.

Triplophyllum centralis (Milne-Edwards and Haime)

Pl. 8, Figs. 10-11; Pl. 10, Figs. 1-7.

Zaphrentis centralis Milne-Edwards and Haime, Mon. polyp. foss. terr. pal., Arch. Mus. Hist. Nat., **5**: 328, fig. 6, 1851.

Zaphrentis centralis Milne-Edwards, Hist. nat. corall., **3**: 336, 1860.

Zaphrentis centralis Worthen, Geol. Surv. Ill., **8**: 72, pl. 9, figs. I—Ia, 1890.

Zaphrentis centralis Keyes, Missouri Geol. Surv., **4**: 112, 1894.

Triplophyllum centralis Simpson, New York State Mus. Bull. **39**: 209, 1900.

Triplophyllum centralis Simpson, Univ. State New York, State Mus. Rept. 54, **3**: 209, 1902.

Description.—The original description of this species by Milne-Edwards and Haime may be translated as follows:

> Corallum a curved cone, moderately elongated, without prominent swellings, have a thin epitheca. Calyx circular; septal fossula large, central, and elongated somewhat toward the side of least curvature; 40 strong and well developed septa, alternately somewhat unequal, and appearing to fall into four groups. Height 3 centimeters; diameter of the calyx 2 centimeters.

Internal characters.—In the neanic stage (Pl. 10, Fig. 7) the cardinal septum is long and heavy, and occupies the entire length of a large fossula. Fosular wall unusually thick, owing to the reënforcement of the septa composing it with secondary deposits of stereoplasm. There are 26 well developed primary septa, those of the cardinal quadrants fusing into the fossular wall, while those of the counter quadrants extend to the alar septa. No secondary septa and but few dissepiments. The septal arrangement is radial in the counter quadrants and pinnate in the cardinal quadrants. Alar fossulae are readily discernible but not conspicuous.

The ephebic stages are illustrated by Figs 2-6 of Pl. 10. In Fig. 6 the septa have increased to about 30, and the radio-pinnate arrangement still prevails. Alar fossulae are now quite distinct. The stereoplasmic thickening of the wall of the cardinal fossula is much less pronounced, and the cardinal septum has atrophied. In Fig. 5 the primary septa number 36, and the alar fossulae are much constricted. Secondary septa now are formed, their insertion apparently having occurred simultaneously between each of the primaries. Disseptiments are few. Fig. 4 shows 44 primary septa and all the secondaries fully developed. The expansion of the calyx has increased the radial symmetry of the septa, which in the cardinal quadrants have receded from their contact with the fossular wall. A considerable open space has formed between the internal end of the cardinal fossula and the distal ends of the primary septa of the counter quadrants. Two major septa (possibly a third pair

of protosepta) play a conspicuous part in walling off the cardinal fossula. Tabulae are well developed, although not visible in the section.

Figs. 1-3 of Pl. 10 show the calyx in stages of full maturity. The septa have continued to become more radially disposed, with accompanying obliteration of the alar fossulae, which, however, are still to be distinguished in Fig. 2. With increasing growth the continued recession of the counter primary septa results in an increasing open area near the center of the corallum. Atrophy has reduced the cardinal septum to a vestige.

Remarks.—The dimensions of the holotype, as given in the original description, are those of a very small (therefore very young?) individual. The average measurement of eight specimens from the Burlington and Keokuk limestones are: mean height: 72 millimeters; mean diameter of the calyx: 33 millimeters.

Hypotypes.—31560 Walker Museum, University of Chicago; 2563 Illinois State Museum.

Horizon and locality.—Burlington limestone, Springfield, Mo., and Sulphur Springs, Mo.; Keokuk limestone, Springfield, Mo.; Chouteau limestone, Knox Co., Mo.

Triplophyllum dalii? (Milne-Edwards and Haime)

Pl. 8, Figs. 1-3; Pl. 11, Figs. 1-7.

Zaphrentis Dalii Milne-Edwards and Haime, Monog. polyp. foss. terr. pal., Arch. Mus. Nat. Hist., **5**: 329, 1851.
Cyathophyllum (fungites?) Owen, Geol. Rep. Wis., Iowa, and Minn., tab. 4, fig. 4, 1852.
Zaphrentis Dalii Milne-Edwards, Hist. nat. corall., **3**: 337, 1860.
Zaphrentis dalei Worthen, Geol. Surv. Ill., **8**: 71, pl. 10, figs. 12–12a, 1890.
Zaphrentis dalei Keyes, Missouri Geol. Surv., **4**: 113, pl. 13, fig. 12, 1894.
Triplophyllum dalei Simpson, New York State Mus. Bull. 39, **7**: 209, figs. 26–27, 1900.
Triplophyllum dalei Simpson, Univ. State New York, State Mus. Rept. 54, **3**: 209, figs. 26–27, 1902.
Triplophyllum dalei Van Tuyl, Iowa Geol. Surv., **30**: pl. 6, fig. 1, 1921-1922.

Description.—Milne-Edwards and Haime failed to figure this species; consequently it can be isolated only on the basis of their description:

> Corallum an elongated cone, curved, gently twisted, and with prominent irregular swellings. Calyx oblique, sub-circular, with a deep cavity. Septal fossula very pronounced, situated on the side of least curvature. 60 to 70 well developed septa, thin, alternately somewhat unequal; the majority extend to the center, where they are a little curved, especially those which adjoin the septal fossula. Height, 5 centimeters; diameter of the calyx 2.5 centimeters. (Translation).

Conspicuous in this description is the large number of septa, which should make the species easy to detect. Actually, however, it seems impossible to find a Mississippian Zaphrentid with as many as 60 septa, and we are left with these alternatives: either Milne-Edwards and Haime erred in counting the septa, or they based their description on a unique specimen. Fortunately the species may be provisionally isolated on the basis of other portions of their description, although Worthen remarks that the *Zaphrentis dalii* com-

monly described from the Keokuk (at the type locality) has only 36 to 42 septa, and is probably actually *Zaphrentis centralis*.

Perhaps the hope of correcting this difficulty led Keyes to emend Milne-Edward's and Haime's description of *Z. dalii*, as follows:

> Corallum simple, large, elongate-conical, more or less curved. Calyx somewhat oblique, sub-circular, deep; septal fossette well defined and located on the side of least curvature. Lamellae 40 to 60 or more in number, rather prominent, thin, somewhat irregular, and usually more or less bent toward the center. External surface rugose, and covered by short, widely scattered spines.

In addition to reducing the number of septa, Keyes supplies a further character in the form of external spines, a feature not mentioned in the original description. In the examination of more than a score of well preserved specimens the writer has discovered traces of external spines in only one, the hypotype described by Worthen. (Pl. 8, Figs. 1-2).

In his *Bibliographic Index of North American Carboniferous Invertebrates*, Weller cites *Zaphrentis spinulifera* Hall as synonymous with *Z. dalii* Milne-Edwards and Haime.[12]

Internal characters.—The early neanic stage illustrated by Pl. 11, Fig. 7, shows 26 strongly developed septa. Six of these are notably thickened: those framing the cardinal and two alar fossulae. Alar fossulae conspicuous, the pinnate arrangement of the septa of the cardinal quadrants standing in strong contrast to the radially disposed septa of the counter quadrants. Epitheca, where preserved, is thin, and a number of dissepiments is discernible. The cardinal septum extends well beyond the center of the corallum, and is heavy and considerably twisted. During later neanic developments (Pl. 11, Figs. 5-6) the principal changes center about the cardinal fossula, which becomes sharply defined and of an elongated pear shape. It is completely bisected by a long, straight, and rather thin cardinal septum. In Fig. 5 the septa have increased to 36, and progress toward radial symmetry is apparent in their disposition. This is specially true of the cardinal quadrants, where the septa have lost much of their pinnate arrangement in spite of their coalescence about the cardinal fossula.

Pl. 11, Fig. 4, exhibits an early ephebic stage. The septa number 40; the attendant expansion of the corallum has greatly lengthened the cardinal fossula, while the insertion of new septa has resulted in a compression of the alar fossulae, which are now somewhat obscured. Bridging the cardinal fossula at intervals are the fused ends of several pairs of adjacent septa, the conjunction of which marked the boundary of this opening during previous stages of growth. The cardinal septum has begun to atrophy, and occupies less than one-half the length of its fossula. Tabulae are more numerous than in any of the previous stages, and the section shows a marked increase in the number of dissepiments. There is no suggestion of secondary septa.

Pl. 11, Figs. 1-3 show successively later stages of ephebic growth. The maximum number of septa achieved is 46, and those of the cardinal quadrants have become elongated to keep pace with the recession of the septa of the

12 Weller, S., Bull. U. S. G. S. No. 153, p. 647, 1898.

counter quadrants. The cardinal fossula has also increased in length proportionally as the calyx expands. Fig. 1 reproduces a section taken immediately below the base of the calyx of an adult form, and it is significant that it reveals no suggestion of the formation of secondary septa. In *Triplophyllum dalii* the development of secondary septa takes place at a late stage of adult life, and their occurrence is commonly limited to the free edge of the corallum surrounding the calyx proper. Once formed, however, they may expand rapidly, and examples are common in which the intercepts of the secondary septa on the upper margin of the corallum are as strong as those of the much older primaries.

Remarks.—The close morphological similarity between *Triplophyllum centralis* and *T. dalii* makes it perhaps desirable that the two forms be compared, and some stress laid upon the differentiating characteristics. Externally these species are alike in being large forms with smooth coralla and lightly imprinted rugae. The epitheca of *T. dalii* is wrinkled and annulated, however, and may show short, scattered spines occasionally somewhat linear in arrangement, whereas the epitheca of *T. centralis* is relatively smooth and is never spinose. Within the calyx, the septa of *T. dalii* are thin, and recurve somewhat before their termination. They remain sharply distinct to their merger in the center of the corallum. The septa of *T. centralis*, as seen in calicular view, are broader and heavier, and disappear before reaching the centr of the calyx, leaving a smooth tabulate area about the cardinal fossula.

In section *Triplophyllum dalii* is distinguished by its long, narrow fossula, frequently showing a bulbous expansion at its inner end, and by the absence of secondary septa in the ephebic and earlier stages. In mature sections the septa of the cardinal quadrants in *T. dalii* remain more closely parallel to the cardinal fossula than do those of *T. centralis;* this phenomenon is produced in part, at least, by the tendency of the former to elongate as the septa of the counter quadrants recede, whereas in *T. centralis* the recession of the counter-quadrant septa produces an open space near the center of the corallum. The septa of *T. dalii* generally have a greater tendency to recurve about the cardinal fossula than do those of *T. centralis*, but this habit is hardly sufficiently pronounced to be considered diagnostic.

Hypotypes.—31546 Walker Museum, University of Chicago; 2556 Illinois State Museum.

Horizon and locality.—Keokuk limestone. Warsaw, Ill., and Crawfordsville, Ind.; Burlington limestone, Springfield, Mo., and Jersey Co., Ill.; Keokuk limestone, Keokuk, Iowa.

Triplophyllum cliffordanum (Milne-Edwards and Haime)

Pl. 8, Figs. 4-5; Pl. 11, Figs. 8-16.

Zaphrentis cliffordana Milne-Edwards and Haime, Monog. polyp. foss. terr. pal., Arch. Mus. Nat. Hist., **5**: 329, pl. 3, fig. 5, 1851.
Zaphrentis cliffordana Milne-Edwards, Hist. nat. corall., **3**: 337, 1860.
Zaphrentis cliffordana Worthen, Geol. Surv. Ill., **8**: 75, pl. 10, figs. 1–1b, 1890.
Zaphrentis cliffordana Whitfield, Ann. N. Y. Acad. Sci., **5**: 576, pl. 13, figs. 1–3, 1891.
Zaphrentis cliffordana Whitfield, Geol. Surv. Ohio, **7**: 465, pl. 9, figs. 1–3, 1895.

Zaphrentis cliffordana Grabau and Shimer, N. Amer. Index Foss., **1**: 58, 1909.
Zaphrentis cliffordana Weller, Bull. Geol. Soc. Amer., **20**: 272, pl. 10, figs. 18-19, 1909.
Zaphrentis cliffordana Butts, Geol. Alabama: 170, pl. 54, fig. 7, 1926.

The original description of this species, by Milne-Edwards and Haime, covers the external characters in considerable detail:

Corallum a curved cone, elongated, without protuberant swellings; epitheca thin, allowing a perception of the serrated ribs (which are) equal, plane, and fairly straight. Calyx circular, quite deep; septal fossula rather large, oblong, situated on the side of least curvature; 32 or 36 sub-equal septa, strong, slightly thickened toward the outside, thinning toward the inside, extending for the most part to the center of the uppermost tabula, upon which they are very slightly curved, and not re-elevated. Their free edge appears obliquely cut. One distinguishes among these septa an equal number of rudimentary septa. Height 3 or 4 centimeters, diameter of the calyx from 1½ to 2 centimeters. (Translation).

To the foregoing description may be appended that given by Weller for the *Zaphrentis cliffordana* of the Fern Glen beds:

Corallum simple, curved, horn-shaped, subcircular in cross-section, expanding somewhat regularly, the sides diverging from the apex at an angle of 35 to 45 degrees, subcarinate along the convex side toward the apex; the axis of the corallum describes a curve which approaches the quadrant of a circle, but which is somewhat more rapidly curved toward the apex. Surface marked by regular annular wrinkles of moderate strength and by almost obsolete longitudinal ribs which correspond in position with septa. Calyx of moderate depth, with a broad base, the fossula of moderate size and depth adjacent to the shorter side of the corallum. Septa in a large individual with a calyx diameter of 20 millimeters, 35 in number without alternating smaller ones; another individual with a calyx diameter of 13 millimeters, has stronger septa with an equal number of small, low septal ridges alternating with them. The septa do not reach the center of the calyx, but leave a smooth clear space in the bottom.

The dimensions of two individuals are: Length of the longer side of the corallum, 44 and 38 millimeters; length of the shorter side of the corallum, 19 millimeters and 19 millimeters; diameter of calyx, 20 millimeters and 13 millimeters.

Internal characters.—Fig. 16 of Pl. 11 illustrates a neanic stage of *Triplophyllum cliffordanum*. In it the septa are seen in the process of insertion in coalesced groups of unequal development. The cardinal septum is strong and extends to the center of the corallum; in addition there appear to be four groups of primary septa of nearly equal development, and four groups seemingly later in origin. There is no suggestion of alar fossulae, and the cardinal fossula can be located only from the position of the cardinal septum. The epitheca at this stage appears moderately thick, but this is due in part, at least, to the obscuring effects of the silicification of the specimen. There are very few dissepiments. Pl. 11, Fig. 15, shows an early ephebic stage. The septa number 21, and are thick and marginally retracted, especially in the counter quadrants. Their disposition exhibits a pronounced radial symmetry. The cardinal septum is abnormally shortened because of poor preservation. The cardinal lateral primaries are in the process of elongation and fusion to form the cardinal fossula. Alar pseudo-fossulae appear to exist, but have not been well preserved. Fig. 14 shows a more advanced ephebic stage, and has suffered some distortion from infiltering silica solutions, which have produced a zonal banding in the open area left by the general marginal retraction of the

septa. The presence of the siliceous replacement material suggests that the center of the corallum was originally filled with stereoplasm, deposited in a kidney-shaped mass about the inner end of the cardinal fossula. Such a conclusion is borne out by the study of other sections. The septa number 32, and have retained the general straightness of the preceding section, but are somewhat less radial in arrangement. A more striking change is the apparent fission of the septa into two component leaflets, a condition especially noticeable in those of the counter quadrants. This appearance seems primarily caused by differential replacement of the original calcareous material. Structureless stereoplasm is more susceptible to siliceous replacement than are organically oriented calcite crystals; there is thus evidence that the septum proper is but a slender blade, thickly covered with stereoplasm.[13] Fig. 13 represents a stage of full maturity. The septa number 36, although the cardinal septum is practically atrophied; an indeterminate number of weakly developed secondary septa is also present. The major septa have failed to elongate in proportion to the expansion of the calyx, and in consequence have undergone a general marginal retraction; they have retained the straightness of the earlier stages, but are relatively broader, and their distal ends are generally free and markedly thickened. Fig. 12 shows a mature stage in a different specimen. The section is noteworthy for the good development of the alar fossulae, the characteristic curved cardinal fossula, with bulbous inner termination , and the absence of secondary septa. The primary septa number 20, and dissepiments are few. Tabulae are well developed throughout the corallum.

Hypotypes.—4704 Walker Museum, Univ. of Chicago.

Horizon and locality.—Fern Glen shale, Kimmswick, Mo., and Sulphur Springs, Mo.; Kinderhook, Monroe Co., and Jersey Co., Ill.

Triplophyllum cliffordanum var. **hespere** var. nov.

Pl. 8, Fig. 6; Pl. 18, Figs. 9-11.

Description.—In external form this variety differs but little from the typical *Triplophyllum cliffordanum*. The only character of note in this regard is a somewhat more rapid bulging of the corallum after the neanic stage, giving the upper part of the cup a rather swollen aspect, and producing a larger calicular diameter than would be found in a typical *T. cliffordanum* of equal length. Variety *hespere* also achieves a larger size than is known for the type form. A mature specimen measured 32 millimeters calicular diameter, 47 millimeters along the concave side and 60 millimeters along the convex side. This specimen possesses 36 major septa, alternating with an equal number of weakly developed secondaries.

The internal characters of the variety are shown in Figs. 8-11 of Pl. 11. The general septal development closely parallels that of *T. cliffordanum*, but the septa assume a decidedly radial symmetry at a very early stage, and the alar fossulae never find a clear expression. It is noticeable in Fig. 10 that the

[13] Compare Frech, F., Zeitschr. Deutsch. Geolog. Gesell., **37**:928-934, 1885.

early quadripartite grouping of the septa is retained into a relatively late period of development, and the pronounced thickening of the distal ends of the septa during the ephebic stage is conspicuous in Fig. 9. The mature section of Fig. 8 is noteworthy for the marked radiality of the septa, and for the comparatively small number of septa possessed at so advanced a stage. The septa are thick and strong, with very wide interspaces, and show a composition similar to those of the type form. The alar fossulae are entirely lacking.

In general characters the variety is such as might be derived from a typical *T. cliffordanum* in consequence of growth to a larger size, with a retarded and accentuated development of the endothecal apparatus through each successive period of growth. The mature stages of *T. cliffordanum hespere* are strikingly similar to the early stages of *Bradyphyllum bellicostatum* Grabau,[14] the principal apparent difference being the development of tabulae in the former.

The specimens upon which the variety is founded occur in the Mississippian (Kinderhook) formation of Lake Valley, New Mexico, and are numbered 31570 of the Gurley collection in Walker Museum, the University of Chicago.

Triplophyllum welleri nom. nov.

Pl. 8, Fig. 9; Pl. 13, Figs. 21-25.

Zaphrentis cliffordana? Worthen, Geol. Surv. Ill., **8**, pl. 10, fig. 1b (not fig. 1), 1890.
Zaphrentis wortheni Weller, Bull. Geol. Soc. Amer., **20**:273-274, pl. 10, figs. 20, 21, 1909.

Zaphrentis wortheni Weller 1909 is preoccupied by *Zaphrentis wortheni Nicholson* 1875[15], hence Weller's species is here renamed *welleri*.

Description.—Weller identifies *Triplophyllum wortheni* as follows:

Corallum horn shaped, the sides diverging at an angle of about 30 degrees. Surface rather smooth, marked by more or less infrequent annular wrinkles which are usually of small size. Rim of the calyx oblique; the calyx deep, contracted below, with a fossula of moderate depth and width toward the shorter, concave side of the corallum; the major septa 25 to 30 in number, their inner extremities extending toward the center of the floor of the calyx, but leaving a small central clear area; between the major septa and alternating with them are an equal number of much lower septa which are sometimes scarcely more than septal ridges.

The dimensions of two individuals are: Length of corallum on convex side, 54 millimeters and 40 millimeters; length of corallum on concave side, 30 millimeters and 17 millimeters; diameter of calyx at rim, 21 millimeters and 18 millimeters. . . . This species includes the straighter individual figured by Worthen under the name *Zaphrentis cliffordana*. It differs from the coral to which that name is here restricted in its much straighter and more elongate form, in the smaller angle of divergence of the sides of the corallum, and in the more oblique position of the calicinal rim.

Internal characters.—Figs. 21 to 25 of Pl. 13 illustrate sections of *T. welleri* from late youth to maturity. In general the endothecal structure of these later ontogenetic stages is identical with that of the Triplophyllid corals already reviewed. The radio-pinnate orientation of the major septa in the

14 Grabau, A. W., Pal. Sinica, B, **2**(2):37, pl. 2, figs. 11 a-e, 1928.
15 Nicholson, H. A., Geol. of Ohio, **2**:235, 1875.

earlier ephebic stages, with subsequent regular increase toward radial symmetry, the progressive atrophication of the cardinal septum, the accentuation of the alar fossulae in the younger portions of the corallum, and the relative paucity of dissepiments are all characters persistent throughout the genus. Significant for the identification of the species, however, are the rather thin and slightly wavering septa, which extend to the center of the corallum and interfuse. Their conjunction may give rise to a dense mass in the center which is roughly crescentiform about the inner end of the cardinal fossula. The formation of secondary septa in an early ephebic stage is sufficient to differentiate this species from *T. cliffordanum*. The shape of the cardinal fossula is not diagnostic, as its curvature and bulbous inner termination strongly suggests that of *T. cliffordanum*.

Remarks.—The similarity of *T. welleri* and *T. cliffordanum* both in appearance and internal structure indicates that they are closely related phylogenetically. They occur together in the Kinderhook strata, and it is not known that one has an earlier range than the other. In the ontogeny of *T. cliffordanum* there is an ephebic stage in which the septa are thick and shortened, and the cardinal fossula weakly developed; such a stage is not present at a comparable period in *T. welleri*. If the shape of the cardinal fossula may be trusted as a biocharacter, its expression in adult sections of *T. cliffordanum* is found repeated in early ephebic sections of *T. welleri*, and thus indicates the latter as the younger species. An alternative inference is the successive derivation of both from a common ancestor which must have been very close to *T. dalii*.

Cotypes.—4705 Walker Museum, University of Chicago

Horizon and locality.—Kinderhook (Fern Glen) Kimmswick, Mo.

Triplophyllum spinulosum (Milne-Edwards and Haime)

Pl. 9, Figs. 1-5; Pl. 12 Figs. 1-11.

Zaphrentis spinulosa Milne-Edwards and Haime. Monog. polyp. foss. terr. pal., Archiv. Mus. Hist. Nat., **5**:334, pl. 5, figs. 7. 7a. 1851.
Zaphrentis spinulifera Hall. Geol. Iowa. **1**(2):650, pl. 22. figs. 1a-b, 1858.
Zaphrentis spinulosa Milne-Edwards, Hist. Nat. Corr., **3**:340. 1860.
Zaphrentis spinulifera White, Am. Jour. Sci. **5**(3):72, 1873.
Zaphrentis spinulosa Worthen. Geol. Surv. Ill., **8**:73, pl. 10. figs. 6-6a, 1890.
Zaphrentis chesterensis Worthen, Geol. Surv. Ill., **8**:73, pl. 9, figs. 3-3a, 1890.
Zaphrentis pellaensis Worthen, Geol. Surv. Ill., **8**:74, pl. 9, figs. 6-6a; pl. 10, figs. 11-11a, 1890.
Zaphrentis spergenensis Worthen, Geol. Surv. Ill., **8**:77. pl. 10, figs. 8-8a, 1890.
Zaphrentis spergenensis Keyes, Missouri Geol. Surv., **4**(2):115, 1894.
Zaphrentis spinulosa? Rominger, Geol. Surv. Mich., **3**(2):152, pl. 54, 5 figs., 1876.
Hapsiphyllum spinulosum Brown, Ann. N. Y. Acad. Sci., **19**:85, figs. 15-16, 1909.
Zaphrentis spinulosa Butts, Geol. Alabama, Sp. Rept. **14**, Ala. Geol. Surv., p. 198, pl. 65, fig. 5, 1926.

Description.—Milne-Edwards and Haime described *Zaphrentis spinulosa* as follows.

Corallum turbinate, moderately elongated, weakly curved and lightly twisted, presenting some irregular swellings and a thin epitheca which upon the parts neighboring

the base forms small conical and sub-spiniform points. Calyx circular, moderately deep; septal fossula moderately developed, situated near the wall, but having a variable position with respect to the curvature; 30 septa, rather thin, very faintly curved near the septal fossula; an equal number of rudimentary septa. Height about 3 centimeters; diameter of the calyx from 1.5 to 2 centimenters. (Translation).

Individuals of this species attain a considerably larger size than is indicated in the preceding description. A large *Triplophyllum spinulosum* from the Paint Creek (Chester) formation measured 60 millimeters along the convex side, 53.7 millimeters along the concave side, and 32.9 millimeters in average calicular diameter. This specimen possesses 42 major septa and an equal number of secondaries. Forms of a similar size are not at all rare.

The numerous small spines to which the species owes its name are arranged upon the epitheca in fairly straight horizontal bands. In each row there are several spines within the space of a centimeter, whereas the vertical distance between succeeding bands is three or four times as great, and increases toward the margin of the calyx. Contrary to the impression gained from Milne-Edwards and Haime's description, the spines are not confined to the vicinity of the base, but may be found on the very rim of the calyx, even in mature specimens. The shape of the corallum varies from nearly straight to gently cornute. The diameter of the calyx increases rapidly after maturity, and forms of large size are decidedly top-shaped.

The species *spinulosum* embraces several distinct varieties, and almost every shade of transition between these. Externally there are no constant characters which distinguish one variety from another, and they can be separated *inter-se* only by studying the internal structure. It would be necessary to section the holotype before the internal characters proper to the species *spinulosum* could be delineated with precision. In the absence of opportunity for this, it is deemed advisable to describe here the two extremes of the observed mutations as variety α and variety β. The septal pattern possessed by the majority of the specimens sectioned is approximately intermediate between α and β; this pattern is shown in Fig. 2.

Hypotypes.—25192 Walker Museum, Univ. of Chicago; 2559 Illinois State Museum.

Horizon and localities.—Kinderhook to Upper Chester, Illinois, Missouri, Iowa, and Arkansas.

Fig. 2. Camera lucida drawings showing the arrangement of the septa as observed in the majority of specimens of *Triplophyllum spinulosum.*

Triplophyllum spinulosum α

Internal characters.—During the neanic period *T. spinulosum α* exhibits a fairly uniform radial distribution of the septa (Pl. 12, Fig. 10) in consequence of the failure of the protosepta to be differentiated from the other primaries, and from the lack of distinct fossular development. At this stage it is frequently necessary to study the exterior of the calyx to determine the position of the cardinal and alar septa. Tabulae and dissepiments are already well developed in the neanic stage.

As the ephebic period is approached, the septa assume the pattern characterizing other members of the genus *Triplophyllum* (Pl. 12, Figs. 3, 4). The cardinal septum is unusual among Triplophyllid corals in that it increases in size during the ephebic period. Similarly, the cardinal fossula is better developed in the sections taken from a stage of early maturity (Pl. 12, Figs. 1, 2). The alar fossulae are formed early in the ephebic stage, and retain their development throughout the remainder of the corallum, being frequently most distinct in the calyx itself (Pl. 9, Fig. 5). With progressive growth the cardinal septum atrophies, and is rarely perceptible in the calyx of an adult.

During the early stages of *T. spinulosum α* the septa are thin and considerably twisted as they approach the center of the corallum. With increase in age they become straighter, heavier, and taper from a proximal thickening. The vertical sections of Figs. 5 and 11, Pl. 12, show the nearly uniform development of tabulae throughout the corallum.

Triplophyllum spinulosum β

Internal characters.—This rarer variety of *T. spinulosum* is shown in Figs. 6-9 of Pl. 16. The neanic stages are essentially similar to those of the first described variety, the divergence of the two becoming marked in the ephebic stages. *T. spinulosum β* differs from *α* chiefly in the configuration of the septa, which in the former are very broad, blade-shaped in cross-section, and taper gradually to a point. The width of the septa constricts the interseptal loculi. The septa converge at the center of the corallum, where their ends twist slightly together. In youthful stages the cardinal septum is slightly longer than the radius of the corallum; it becomes recessive with maturity. In the older portions of the corallum the broad septa crowd the alar fossulae out of existence, but in the early ephebic stages, before the septa have achieved their full width, the alar fossulae are clearly visible. Tabulae are less numerous than in variety *α* and dissepiments are of comparatively rare occurrence. As may be seen in Fig. 6, a section cut immediately below the calyx, the thickness of the septa is not conspicuous in the calyx itself. Secondary septa develop at a late stage, and are confined to the calicular wall.

Remarks.—The examination of hundreds of specimens of *T. spinulosum* shows that *Zaphrentis spinulifera* Hall is synonymous with *Triplophyllum spinulosum* (E. & H.). Hall's description of his species is:

> Coral in the form of a reversed cone, curved. Calyx slightly oblique, circular or sub-circular, the cavity deep; septal fossette strongly marked, situated on the inner side

of the curvature. Radiating lamellae strongly defined, somewhat irregularly curved, numbering at the margin from forty-two to fifty, and uniting in fascicles of two, three, four or more before reaching the center; outer walls of the calyx thin at the upper margins, becoming very thick and strong below. Externally somewhat rugose, and often swelling abruptly at intervals; the stages of growth marked by somewhat regular rows of nodes or short spines.

The exact systematic position of *Z. spinulifera* has long been in dispute. Worthen concluded that it must be identical with *Z. dalii* E. & H., and remarks:

This description (of *Z. dalii*) corresponds well with the form described subsequently as *Z. spinulifera*, the principal difference being in the larger number of lamellae in E. & H.'s specimen. This character, however, is a variable one, and as there is no other form known from that locality that has even as many as fifty lamellae, it becomes almost certain that their specimen was specifically identical with that subsequently described as *Z. spinulifera*.[16]

Worthen seems to have reached his conclusion chiefly because of his inability to attribute as many as 42 septa to *Triplophyllum spinulosum;* and a careful examination of his hypotype for *Z. spinulifera* (Pl. 8, Fig. 12) shows that he was further deceived through identifying a large *T. spinulosum* as *T. dalii.* It has already been remarked, however, that examples of *T. spinulosum* possessing 42 or more septa are fairly common in numerous Chester horizons, and also at Hall's type locality at Warsaw, Illinois, whence came Worthen's hypotype. In every external detail these large forms are strikingly similar to Hall's figure of *Z. spinulifera,* and there seems, therefore, to be no tangible reason for maintaining the specific distinction of the latter. A similar conclusion was reached by Keyes, who remarks:

Hall's form, *Z. spinulifera*, originally described from Warsaw, Illinois, is without doubt identical with the species under consideration (*Zaphrentis spinulosa* E. & H.), and is so regarded here.[17]

Keyes did not cite the evidence which led him to this conclusion.

Certain other of the Mississippian species described by Worthen in volume 8 of the Geology of Illinois are here considered as synonymous with *T. spinulosum: Zaphrentis chesterensis* is described by Worthen as follows:

Corallum elongated, moderately curved, gradually and regularly tapering; calyx circular, not deep, fossette deep, and situated on the side of shortest curvature. Lamellae in four divisions, the two on either side of the fossette to the number of seven or eight coalesce before reaching the bottom of the calyx. On each side of the strong septum opposite the fossette, there are twelve or thirteen lamellae that extend singly to the bottom of the cup. Surface slightly rugose, with traces of short spines scattered irregularly over it.

This is a variety of *Z. spinulosa*, E. & H., but may readily be distinguished by its more elongated and symmetrically tapering form, and the greater number of lamellae.

Worthen's holotype has been carefully studied, and possesses no character justifying the separation of *Z. chesterensis* as a species distinct from *T. spinulosum.* (Pl. 9, Fig. 2.). The above description of the septal apparatus of *Z.*

16 Worthen, A. H., Geology of Illinois, **8**:72, 1890.
17 Keyes, C., Missouri Geol. Surv., **4**:114, 1894.

chesterensis is equally applicable to *T. spinulosum*, differing from the arrangement in that species no more than its individual members might differ from each other. The characters cited as identifying *Z. chesterensis*, namely, its large number of septa and its elongated and symmetrically tapering form, do not, as revealed in the holotype, form the basis for a new species. They are repeated among the members of the type species with sufficient frequency, however, to constitute a recognizable variety.

The conclusions stated above for *Z. chesterensis* Worthen apply with equal force to *Z. pellaensis* Worthen. The description of this species is:

> Corallum turbinate, regularly curved, height of an average specimen 1⅜ in., diameter of calyx about ¾ in., depth of cup ⅜ in.; sides descending abruptly, the lamellae on each side of the fossette to the number of four or six coalescing, while the others extend singly nearly to the center of the cup. Fossette narrow and situated obliquely to the curvature of the corallum. Whole number of principal lamellae 32 to 36 with about the same number in the secondary series. Surface moderately rugose, and often marked by a few short scattering spines that are usually restricted to the lower portion of the corallum.
>
> This form is closely related to *Z. spinulosa* E. & H. from the Chester beds, but is usually shorter in proportion to its diameter, and coming from a different geological horizon it is entitled to be considered as a distinct variety.

An examination of the cotypes (Pl. 9, Figs. 3-4) fails to reveal any characters distinguishing *Z. pellaensis* from *T. spinulosum*. The internal structure of this species is that of *T. spinulosum;* its proportions, which are duplicated by large numbers of individuals of *T. spinulosum*, would permit its retention as a variety of that species. Stratigraphic position can scarcely be considered a character of specific worth, and Worthen's use of it as such in this case is in disregard of the long range of *T. spinulosum*. It is also true that the attributes of form which distinguish Worthen's species are not confined solely to corals from the Pella beds, but are found in individuals from a variety of horizons.

Zaphrentis spergenensis Worthen is also here held to be synonymous with *Triplophyllum spinulosum* (E. & H.). Although the holotype of this species has been lost, at least temporarily, Worthen's figures and description indicate that *Z. spergenensis* is certainly a *Triplophyllum*, and almost equally certainly a young individual of *T. spinulosum*.

Triplophyllum illinoisense (Worthen)

Pl. 8, Figs. 7-8.

Zaphrentis illinoisensis Worthen, Geol. Surv. Ill., 8:77, pl. 9, figs. 4-4a, 1890.
Zaphrentis illinoisensis Keyes, Missouri Geol. Surv., 4:112, 1894.

Description.—Worthen's original description is:

> Corallum very broadly turbinate, cup oblique, surface marked by several transverse undulating ridges and numerous longitudinal striae. Septal fossette deep and situated on the side of least curvature; lateral fossettes narrower but distinct, separating the lamellae into three well marked divisions, the two on either side of the septal fossette consist of ten or eleven each, making thirty-eight to forty primary lamellae in the entire cup.

This species was evidently sessile, and was attached near the lower extremity to some cylindrical body, the scar of attachment being visible on nearly all the individuals seen.

Length of a large individual 2⅞ in., breadth of cup 2 and 1-16 in.; depth of same about 1 in.

Remarks.—The unusually broad, deep calyx of *T. illinoisensis* excellently illustrates the characters of the genus *Triplophyllum.* The cardinal fossula is of exceptional width and depth, and extends slightly beyond the center of the calyx; it expands noticeably toward its internal termination. The two alar fossulae, likewise strongly developed, merge with the cardinal fossula at the center of the calyx, joining it at angles of about 60 degrees. The juncture of these three produces an open area at the center of the calyx of such size as to greatly increase the apparent calicular depth.

The primary septa are exceptionally thick, but the calyx flares out so broadly that their proximal ends are not crowded, and the interseptal spaces are much wider than is common in a form possessing as many as 20 septa. This latter phenomenon has an unusual effect upon the rugae or external striations upon the corallum, giving them the appearance of double lines ruled at intervals upon the epitheca, rather than the customary unilinear appearance. The cardinal septum is completely aborted in the post-neanic stages.

Triplophyllum illinoisensis is closely related to *T. centralis;* the two differ chiefly in those features attendant upon the much greater expansion of the calyx in the former.

Holotype.—2562, Illinois State Museum, Springfield, Ill.

Horizon and localities.—Keokuk limestone, Warsaw, Ill., and near Plymouth, Hancock Co., Ill.; Wayland, Clark Co., Mo.; Keokuk and Bonaparte, Iowa.

Genus **Homalophyllum** Simpson emend. Grove

Homalophyllum Simpson, New York State Mus. Bull. **39**, **7**:221, 1900.
Homalophyllum O'Connell, Annals New York Acad. Sci., **23**:192, 1914.

Genotype—Zaphrentis ungula Rominger, Geol. Surv. Mich., **3:** 181, 1876. Onondaga limestone.

Example.—Zaphrentis herzeri Hall, Fossil corals, Niagara and Upper Held. Groups: 35, 1882.

Description.—Corallum cornute, but asymmetrically flattened on the cardinal (convex) side. Calyx sub-oval to round. Primary and secondary septa well developed, the former reaching to the center of the calyx, where they may recurve slightly upward. Cardinal fossula moderately large, extending to the center of the calyx on the convex side. Tabulae and dissepiments occur, but are not conspicuously developed. The members of this genus show no evidence of an operculum at any stage of development.

Simpson's original description of this genus is:

The above species *(Zaphrentis ungula* and *Z. herzeri)* have a decided characteristic in that they are flattened on the side of greatest curvature; for some distance from the apex they are concave; calyx oval, with one side straighter than the opposite side. The form of the corallum is similar to that of *Calceola.* They make a natural group which differs from *Zaphrentis,* and should be removed from that genus.

Homalophyllum calceolum (White and Whitfield)

Pl. 9, Figs. 20-24; Pl. 13, Figs. 1-6.

Lophophyllum calceola White and Whitfield, Proc. Bost. Soc. Nat. Hist. **8**:305, 1862.
Zaphrentis calceola White, Cont. Invert. Paleon., No. 8, in, Hayden, U.S.G.S. Surv. Terr. Wyoming and Idaho; 156, pl. 39, figs. 6a-d, 1880.
Zaphrentis calceola Rowley, Am. Geol. **3**:275, 1889.
Zaphrentis calceola Keyes, Missouri Geol. Surv., **4**(1):110, 1894.

Description.—In their original description of this species, in 1862, White and Whitfield assigned it to the genus *Lophophyllum*. Later perceiving this to be an error, White redescribed it in 1880, placing it in the genus *Zaphrentis*. His revised description is:

> Corallum small, subturbinate, more or less curved, moderately but irregularly expanding from the base or apex upwards, flattened on the outer side of the curvature, especially at the lower portion, but elsewhere somewhat regularly rounded; apex small, pointed; exterior surface rugose from unequal growth; calyx moderately deep; fossette situated subcentrally, but extending towards the side of the convex curve of the corallum; principal rays about thirty; secondary rays about equal in number with the principal ones, but they are usually very small and inconspicuous.
>
> Extreme length of an average example, 18 millimeters; diameter of calyx, about 9 millimeters.

As originally described, this form differed from its all too numerous fellows in the genus *Zaphrentis* chiefly in the marked flattening of the convex side. An inspection of the calyx reveals yet further departures from the characters attributed to the genus *Zaphrentis*, though the external asymmetry of the corallum first commands attention. The flattening of the convex side thus indicated is greatest at the tip, and becomes gradually less pronounced with growth, so that a mature calyx may present a cross-section which is essentially circular. The corallum of *Homalophyllum calceolum* is also marked externally by a series of alternating constrictions and swellings, of unusual regularity, which begin a short way above the tip and continue to the rim of the calyx. These annulations, which may possibly be indicative of periodic rejuvenation, are noteworthy for the marked parallelism of each of the constricting bands.

The calyx of *H. calecolum* is moderately deep, and in a mature specimen there are from 30 to 36 well developed major septa and an equal number of short secondaries. The septa are nearly radially disposed, and the primaries extend well toward the center of the calyx, but before reaching the center they recurve slightly upward and coalesce. As a result the center of the calyx is composed of the fused ends of the septa, apparently reënforced by deposits of stereoplasm, thus forming a protuberance raised somewhat above the remainder of the calicular floor. The structure resulting is in many respects suggestive of an incipient columella, but at no stage of development is it sufficiently marked to be termed columelloid. As can be seen in the serial sections reproduced in Figs. 1-5 of Pl. 13, *H. calceolum* does not deviate markedly from the general pattern of the tetracorals in the appearance of its calyx. In addition to the arrangement of the septa already described, there exists a well-developed cardinal fossula which preserves its strength through

all but the earliest stages of the corallum. The cardinal septum, when first visible, extends the full length of its fossula, and subsequently undergoes the progressive atrophication observable in many of the *Zaphrentidae*. Tabulae and dissepiments are not perceptible in any of the serial sections, but their absence is due to poor preservation.

From the orientation afforded by a study of the septal arrangement, it is seen that the flattened side of the corallum is the cardinal side.

When, however, the tip of the corallum, which is characterized by the maximum degree of external asymmetry, is examined in section, the internal structure is found to differ greatly from that of the later and more cylindrical portions. (Pl. 13, Fig. 6). The septa of this neanic stage are short and chaotic in arrangement. Of the primary septa, only the cardinal septum is outstanding; there is little suggestion of a fossula, and the entire center of the corallum is open.

Hypotypes.—31584 Walker Museum, University of Chicago.

Horizon and Range.—Chouteau limestone, Sedalia, Missouri.

Relationships of Homalophyllum calceolum.—In the morphology of *H. calceolum* there are two dominant trends: A columella-like fusion of the major septa in the center of the calyx; and a tendency to flatten the convex side of the corallum. The first of these is best expressed in the more mature portions of the individual, whereas the second is pronounced only in the earliest stages. The determination of the generic position of the species rests upon the evaluation of both of these factors, and the study of their closest affinities among other tetracorals.

As has been noted, the first of these trends, that of a columella-like coalescence of the septa, is weakly developed. The structure produced is never strongly demarcated, and comes into existence only in the maturity of the individual. If this were a vestigal heritage, in the slow process of atrophication, its development should at least remain uniform throughout the corallum, or rather become somewhat feebler with increase in the age of the individual. The fact that the reverse condition prevails seems to indicate that this is a morphological unit in the process of formation a structure whose fulfillment is to be sought in the progeny, and not the ancestry, of the species under observation. It has often been noted that the later Carboniferous corals are characterized by the widspread development of columellae, and it may be that the structure here described is an early forshadowing of such a trend. There is, however, considerable opposition to the unqualified adoption of such a view. A tendency of the septa to recurve upwards into a columelloid structure is noted by Milne-Edwards and Haime in their description of the genus *Cyathophyllum:*

> Cloisons bien developpées et s'étendant jusqu'au centre du calice, ou èlles sont légèrment courbées et relevées de manière a produire quelquefois l'apparence d'une columelle rudimentaire. (Milne-Edwards, Histoire Naturelle des Coralliaires, 3:364.)

A similar septal structure is noted by Hall in a number of the species of *Zaphrentis* which he describes from the Devonian Falls of the Ohio.[18]

18 Hall, J., 12th Ann. Rept. Ind. Dept. Geol. Nat. Hist. pp. 285-297, 1882.

In consequence of these several possible interpretations, this peculiarity of the septa can scarcely serve as an index to the generic position of *H. calceolum,* and seems rather a feature of homeomorphy, since a somewhat similar structure is remarked for the primitive genus *Streptelasma* Hall. It is, therefore, to the trend manifested in the flattened cardinal side that we must turn as an initial means of isolating the forms congeneric with *H. calceolum.*

The list of North American corals exhibiting a flattening of one side is not lengthy, but when it is combined with that of similar forms known from other parts of the world, a very considerable number of species is embraced. Our terminology does not provide us with a means of designating this group as a whole, yet there is a definite need of avoiding the clumsy redescription of these corals each time it is desired to refer to them collectively. This need has been recognized by the Germans, who indicate them as "*Pantoffel* (slipper) corals." If only for phonetic reasons, this word is scarcely suitable for adoption into English terminology, and in its place the term "calceoloid corals" (Latin *calceolus*—a little shoe) is here proposed. This designation has the dual advantage of being based on the most conspicuous morphological feature of the group, i. e., their slipper-like shape, and of suggesting their most typical representative, the familiar genus *Calceola* Lamarck.

Among the North American representatives of the calceoloid corals are the following genera and species:

Calceola attenuata Lyon—(Niagaran, Kentucky, Tenn.)
C. coxii Lyon—(Niagaran, Tenn.)
C. cornicula Lyon—(Niagaran, Tenn.)
C. tennesseensis Roemer—(Niagaran, Kentucky, Tenn.)
Halophragma calceoloides Lds.—(Upper West Union Fm., Ohio)
Cyathophyllum exiguum Billings—(Onondagan, Ohio, Ontario)
Homalophyllum herzeri Hall—(Onondagan, Ohio)
H. ungulum Rominger—(Onondagan, Ohio, Miss. valley)
H. calceolum Wh. and Whit.—(Chouteau Is., Indiana, Missouri)
Zaphrentis compressa Rominger—(Onondagan, Ohio).

Even a cursory inspection of the superficial characteristics of this assemblage permits it to be separated into several constituent groups: *Calceola tennesseensis, C. cornicula, C. coxii,* and *C. attenuata* all possess opercula, and in each of these species the counter side is the flattened side.[19] Their proper position in the genus *Calceola* is therefore apparent.

Halophragma calceoloides is flattened on the cardinal side, and does not possess an operculum at least in mature stages. This coral was first described by Lindström, who attributed to it an origin indepenedent of the *Calceolidae.* Its peculiar form has been interpreted by Richter, who says of it:[20]

> This species builds itself a sharply bounded *Calceola*-like corallum, but in about the second half of its growth bends itself upwards and takes on a circular cross-section . . . There is exhibited, in each individual corallum of *Halophragma*, through the loss of the slipper shape, the exact point in time in which the operculum weakened or

19 Lyon, Proc. Nat. Acad. Sci. Phila., **1879**:43 ff.; Roemer, Lethea Geognostica, **2**:385, 3 ed.; Safford, Amer. J. Sci. **29**(2):248, 1860.

20 Richter, R., Die Verhältnisse von Funktionen und Form bei den Deckelkorallen, Senckenbergiana **11**:71-72, 1929.

entirely lost its articulated movement, and with this its formational power. (Writer's translation).

In *Homalophyllum herzeri* the flattening of the corallum is also on the cardinal side, a condition likewise true of *H. ungulum*. The endothecal apparatus of these two species is that normal to the *Zaphrentidae*, and only their flattened coralla make them conspicuous. Both forms possess very deep calices, with a large number of well developed septa, and both have conspicuous cardinal fossulae.

Cyathophyllum exiguum[21] has 35 to 40 septa and a cardinal fossula of moderate size. Its most notable character is the unusual flattening of the cardinal side. In many individuals this feature is so developed as to leave no doubt of its purpose—that of insuring the calyx of an upright orientation. The major septa of *C. exiguum* recurve upwards near the center of the calyx into a columelloid structure very similar to that already described for *Homalophyllum calceolum*.

Zaphrentis compressa Rominger is a species whose morphological characteristics are essentially like those of *Homalophyllum ungulum*.[22]

From the preceding considerations there arises two possible ways of explaining the community of shape possessed by calecoloid corals: (1) It may have been acquired by heritage from a common ancestry, however remote; (2) Environmental adaptations may have impressed upon corals of various lineages a common similarity of external form.

The morphology of the operculated corals has been very carefully studied by Richter,[23] and he has advanced the theory that the flattened side of an operculated coral has arisen as a consequence of the mechanical necessity of a straight hinge line for the articulation of an operculum. Richter opposes the theories of Walther, Yakowlew, and Dacqué, each of whom holds a modification of the idea that the flattened side of the corallum has arisen as a means of giving it definite orientation, i. e., as a "resting surface." As contrary evidence, Richter cites the fact that operculate corals which become colonial, or which develop supporting roots, persist in retaining their calceoloid shape. Among North American corals this phenomenon is especially well manifested by *Calceola attenuata* Lyon.

Richter's theory is plausible in its application to corals which are known to have possessed opercula, but there is also evidence to show that flattened coralla may arise without the functional control of an operculum. Of the forms whose morphology has just been briefly reviewed, *Homalophyllum herzeri, H. ungulum, H. calceolum, Cyathophyllum exiguum* and *Zaphrentis compressa* possess endothecal apparati so well developed as to preclude the idea that they were operculate at any stage in the development of the indi-

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21 Lambe, L., Cont. to Can. Pal. 4(2):150, 1901.

22 Hall, J., 12th Rept. Ind. Dept. Geol. Nat. Hist.: 295, pl. 21, figs. 4-5; pl. 22, fig. 5, 1882. Rominger's name is preoccupied by *Zaphrentis compressa* Milne-Edwards and Haime, 1860.

23 Richter, R., op. cit., pp. 56-94.

vidual. That the flattening of *C. exiguum* is essentially related to orientation seems obvious from the direct relationship between the degree of flattening and the position of the calyx. The end point of such a functionally controlled flattening is found in the genus *Palaeocyclus*. Grabau[24] notes that certain modern corals, such as *Manicina*, show a flat base when found upon a hard, sandy sea bottom, while others of apparently the same species develop a pointed corallum when the bottom is of soft materials into which they can sink slightly.

It seems logical to conclude that the calceoloid corals are a polyphyletic group whose convergence is the result of a superficial form impressed by several factors. In the *Calceolidae* and *Halophragma* the shape is a functional accessory of the operculum; in *Cyathophyllum exiguum* the flattening is an adaptation resulting in an upright position of the calyx. In *Homalophyllum calceolum*, *H. herzeri*, and *H. ungulum* the flattened side appears to be a heritage evidencing true generic relationship, since these corals are not operculated, and the degree of flattening is not sufficient to have an appreciable effect on the position of the calyx.

It is not possible to do more than speculate as to the ancestry of these three latter forms, but *Halophragma* is a logical candidate for this position. *Halophragma* has already been cited as a form evidencing transition from operculated to non-operculated types. Its endothecal structure needs but little modification to give rise to that of *H. herzeri* or *H. ungulum*, and indeed it is almost recapitulated in the early stages of *H. calceolum*. Lastly, it is properly placed in time to have been ancestral to the Devonian forms.

In erecting the genus *Homalophyllum* Simpson perceived the close relationship existing between *Zaphrentis herzeri* and *Z ungula*, but his diagnosis of the genus does nothing more than to define the calceoloid corals as a whole. Even the *Calceolidae* are not excluded, except by implication. . In the preceding discussion it has been shown that the calceoloid corals are not entirely congeneric; Simpson's definition of *Homalophyllum* should therefore be reworded so as to include only those species which are truly related. To that end the foregoing emendation has been proposed.

Genus **Neozaphrentis** gen. nov.

Genotype.—*Zaphrentis tenella* Miller, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res., p. 621, pl. 1, figs. 17-18, 1891.

Description.—Small to large conical to sub-cylindrical solitary corals, curved or nearly straight. Exterior rugose and may be concentrically wrinkled and undulatory; often annulated from rejuvenescence or periodic growth. Calyx shallow to deep. Septa variable in thickness, smooth, non-carinate, straight or distally wavering; in two cycles, but the secondaries may be rudimentary. Not more than 60 major septa, not marginally retracted, extending to the center of the calyx where they may fuse, or disappearing a short distance before reaching the center, which is then occupied by a small open or tabulate area. Cardinal septum recessive in post-neanic stages. Cardinal

[24] Grabau, A. W., Pal. Sinica, B, 2(1): 5-6, 1922.

fossula well developed, variable in position, sub-central or extending to the margin. Tabulae few or numerous, partitioning the whole of the corallum; dissepiments few, and not arranged in definite zones. No columella or central columelloid structure resulting from the fusion of the septa.

Remarks.—O'Connell's revision of the genus *Zaphrentis* seems definitely to establish its type species (*Z. phrygia* Raf. & Clif. = *Caryophyllia cornicula* Leseur) as a form with carinate septa.[25] Accordingly, only by error or oversight could any of the several hundred species assigned to this genus be rigorously considered as belonging therein. The extremely generalized wording of Rafinesque and Clifford's generic description has made *Zaphrentis* easily applicable to a wide variety of tetracorals of primitive type, and in addition the genus has formed a convenient dumping ground for forms apparently lacking in distinctive generic characters.

Milne-Edwards and Haime, Thomson and Nicholson, Carruthers, and numerous other writers have published emendations of the original description of *Zaphrentis*, each endeavoring to include or emphasize those characters which he believed Rafinesque and Clifford meant to pertain to *Zaphrentis*, but failed to note. There have thus grown up definitions of *Zaphrentis sens. lat.*, which, while conforming to a certain general pattern, are readily pliable, and have no precise demarcations except such as may exist in the mind of the individual worker. Evidence of the plasticity of such generic concepts is found in the fact that during the past half century no less than ten genera have been created out of species originally assigned to *Zaphrentis*, and yet but a small fraction of its species has been critically revised.

On the other hand, a tabulation (biometric and morphological) of the characters of 100 species of *Zaphrentis* drawn at random from the works of Milne-Edwards and Haime, Hall, Greene, Worthen, and Miller, leaves no doubt but that a larger number of these forms are congeneric. It appears from this that the popularity of *Zaphrentis sens. lat.*, as evidenced by its widespread usage, arises only slightly from its adaptability to the eccentricities of doubtful species, and essentially because there exist large numbers of tetracorals, truly congeneric, whose generic characters are those of *Zaphrentis* as it is commonly interpreted.

In view of the establishment of *Zaphrentis* in the literature, it may, at first thought, seem advisable to continue the usage of *Zaphrentis sens. lat.* as the generic designation for these species, separating, as the occasion arises, such forms as are found to be generically distinct. Such indeed has been the procedure during the past twenty years. The objections to this method are two: (1) *Zaphrentis sens. lat.* is practically and taxonomically unsound, in that it does not and cannot have a type species. (2) The characters of *Zaphrentis sens lat.* must always be, in final analysis, the result of individual interpretation. Hence it seems better to create new genera, even based on characters of uncertain final value, than to assign species to a genus whose position is doubtful, and whose characters are undetermined.

In the course of the present revision, *Zaphrentis tenella* Miller was found

25 O'Connell, M., op. cit., p. 182.

to be a species whose generic structure coincides with the prevailing generalized interpretation of *Zaphrentis* Raf. & Clif., yet differing from *Z phrygia*, the genotype. The description of *Neozaphrentis*, while drawn from the type species, is therefore essentially that of *Zaphrentis sens. lat.* It is hoped that there may thus be provided a taxonomically sound repository for large numbers of congeneric species now termed *Zaphrentis*.

Neozaphrentis tenella (Miller)

Pl. 9, Figs. 6-8; Pl. 13, Figs. 7-14.

Zaphrentis tenella Miller, Adv. Sheets, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 11, pl. 1, figs. 17-18, 1891.
Zaphrentis tenella Miller, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 621, pl. 1, figs. 17-18, 1892.
Zaphrentis tenella Keyes, Missouri Geol. Surv., **4**:111, pl. 13, fig. 10, 1894.

Description.—Corallum simple, turbinate, twisted, moderately curved, regularly enlarging and tapering to an acute point at the base. Surface marked by shallow constrictions of growth and smaller concentric wrinkles. Epitheca not preserved. Calyx deep, very slightly inclined to the long axis of the corallum or nearly transverse, outer wall thin. Septa equal, moderately large, and uniting around a subcentral fossula, that extends to the wall, on the left side of the corallum, and embraces a rudimentary septum. There are twenty-six septa in the specimen illustrated, which is .35 of an inch in diameter.

This species is distinguished by its elongated form, long tapering point and number and position of the septa and fossula

To Millers' above description certain additional diagnostic features may be added. The curvature of the corallum in *Neozaphrentis tenella* is frequently modified by a sharp twist of the tip portion (Pl. 9, Fig. 8) at nearly a right angle. In every individual examined, this twist was toward the right side when the corallum was oriented with the cardinal fossula upward. There seems evidence that the bending of the corallum which produces this twisted tip takes place relatively late in life, as young individuals are quite straight. The apparent uniformity in direction of twisting suggests that it was a means of insuring a definite orientation of the calyx. When the calyx is oriented as above, the cardinal fossula is commonly observed to be displaced toward the left side, although in some specimens it is nearly central in position, and even rarely on the right side.

In mature specimens the primary septa may number as many as 34. Secondary septa are usually absent, even in adults; when visible, they exist as tiny denticulations of the calcinal margin. The cardinal septum is early recessive; the alars are in no way distinguished from the other primaries. The counter septum, in well preserved adults, is the largest and longest septum of the calyx, and stands noticeably higher than the remainder. Hypertrophy of the counter septum is not noticeable in young specimens, and seems associated with the bending over of the corallum, perhaps in the manner suggested by Yakowlew.[26] Dissepiments are exposed where the epitheca has eroded away, but are seldom visible in transverse section. Tabulae occur at

[26] Yakowlew, N. N., Geol. Mag., **4**(6):108-115, 1917.

rather wide intervals, but partition the corallum completely where they exist.

Internal characters.—(Pl. 13, Figs. 7-14.) In neanic stages the septa display nearly radial symmetry, modified only by a tendency of those of each quadrant to fuse together. They extend well toward the center of the corallum, where their inner edges coalesce, leaving a circular opening bounded by a stereotheca. With expansion of the corallum, this central opening merges with the cardinal fossula, giving this an expanded inner termination. This structure is generally persistent into the adult, except as obscured by tabulae and by the transgression of the counter septum. In youthful stages the cardinal septum extends to the center of the corallum, where it joins the stereotheca; it is somewhat thinner than the other primaries and is rapidly recessive, having nearly disappeared at the close of the neanic stage.

During the ephebic and later periods the radial arrangement of the septa in the cardinal quadrants gives way to a pinnate disposition about the cardinal fossula. The counter septum becomes elongated and thickened, and extends well into the open center of the corallum. Its position is usually excentric,, either to the right or left of a line bisecting the cardinal fossula.

Remarks.—Some stages of *Neozaphrentis tenella* bear a strong resemblance to *Zaphrentis konincki* Edwards and Haime, but the former is much smaller when at the stage of similarity, and possesses a much better developed fossula.

Hypotypes.—31593 Sampson Collection, Walker Museum, University of Chicago.

Horizon and localities.—Chouteau limestone, near Sedalia, Mo., Kinderhook limestone, Louisiana, Mo.

Family *Hapsiphyllidae* Grabau

Simple corals, usually of small size, and of conical or horn-shaped form, straight or curved. Epitheca with growth lines, often with wrinkles and with the septal grooves well marked. In some forms the surface is covered with strong hollow spines. Counter quadrants accelerated, often strongly so, containing in extreme cases four times as many secondaries as the cardinal quadrants. Cardinal septa united by their inner ends to form a secondary wall or phyllotheca, which may also include the alars and secondaries of the cardinal quadrants. The wall may be incomplete, open on the cardinal side with the cardinal septum projecting into the gap or shortened to form a cardinal fossula; or it may be modified by the thickened ends of the septa, or by the development of a median mass of stereoplasm more or less crescentic in transverse section. Tertiary septa indicated or moderately developd. Tabulae when present restricted to the inner area; dissepiments present in most cases, but not abundant.

Genus *Hapsiphyllum* Simpson

Hapsiphyllum Simpson, New York State Mus. Bull. **39**:203, fig. 10, 1900.
Hapsiphyllum Grabau, Pal. Sinica, B, **2**(2):118-120, fig. 21, 1928.

Genotype.—*Zaphrentis calcariformis* Hall, Fossil corals, Niagara and Up. Helderberg groups, p. 33, 1882, and 12th Rept. Indiana Dept. Geol. Nat. Hist., p. 293, pl. 21, figs. 10-11, 1882.

Original description.—Corallum simple, conical or horn-shaped; calyx circular, comparatively deep, with thin margins; biareal. The outer area is bounded by the external epitheca; the inner area by a sub-vertical wall of horseshoe shape, open on the side of the septal fovea. Two larger septa connect with this wall in such a

manner as to apparently be a continuation of it, and form a very distinct pyriform septal fovea; sept alternating in size, the smaller ones continuing for a short distance into the cavity of the corallum, there coalescing with the larger ones, which continue to the inner wall, with which they coalesce, and in which they terminate. Tabulae and dissepiments are present.

The wall of the inner area, connecting with two of the septa and bounding a portion of the septal fovea, is similar to that of *Agonophyllum*, but that genus differs from this in several respects, principally in having carinations on the side of the septa.

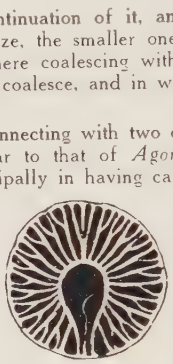


Fig. 3. Cross-section of *Hapsiphyllum calcariforme* (Hall) showing the characters of the genus *Hapsiphyllum*. (After Simpson).

The phenomenon of septal acceleration, which in the hands of Grabau and his students has been given widespread application as a means of characterizing coral genera and species, is described by him in the genus *Hapsiphyllum* as follows:

In the genotype, *H. calcariforme* there are 13 septa between the cardinal and counter on each side, making 12 secondaries, but their distribution in the quadrants is not determined. The probabilities however, judging from analogy with other species are that there are four in the cardinal and eight in the counter. The tertiary septa[27] all adhere to the secondaries in the type species, the counter septum having one on each side which is longer than that found in the other septa. In European species however, the tertiary septa are most usually free and often only very slightly developed. The cardinal septum in the type species is very short, but in European and Asiatic species it is often long.

Hapsiphyllum cassedayi (Milne-Edwards)

Pl. 9, Figs. 18, 19, 25; Pl. 13, Figs. 15-20.

Zaphrentis cassedayi Milne-Edwards, Hist. nat. corr., **3**:341, pl. G1, fig. 2, 1860.
Zaphrentis prona Milne-Edwards, Hist. nat. corr., **3**:342, 1860.
Zaphrentis calcariformis Hall, 12th Rept. Indiana Dept. Geol. Nat. Hist.: 293, pl. 21, figs. 10-11, 1882.
Zaphrentis ulrichi Worthen, Geol. Surv. Illinois, **8**:76, pl. 10, figs. 10-10a, 1890.
Zaphrentis cassedayi Greene, Contrib. Indiana Pal., pt 18: 178, pl. 52, figs. 12-18, 1904.
Zaphrentis cassedayi Beede, 30th Rept. Indiana Dept. Geol. Nat. Res.: 1203, pl. 7, figs. 3-3c, 1905.

Description.—Corallum regularly conical, pointed at the base, straight or a little curved. Growth annulations very slightly pronounced. The entire surface is covered with small conical spines, fairly regularly spaced. Calyx circular and deep. Septal fossula large, oblong, very deep, centro-lateral. 24 principal septa, thin, a little unequal, obliquely fusing together by their inner edges, in such manner as to form the wall of the septal fossula. An equal number of septa also well developed, but a little smaller

27 As used by Grabau the term "primary septa" refers only to the four first formed septa of the corallum—the cardinal, counter, and two alar septa. The remaining septa of the first cycle he designates as secondaries, and those of the succeeding (2nd) cycle as tertiaries.

than the preceding ones. When the calyx is placed before the observer in such fashion that the lateral prolongation of the central fossula is downward, one sees that each one of the small septa unites with its large neighbor on the right, in the right-hand portion of the calyx, and with its large neighbor on the left in the left-hand portion. The height of the corallum is about 2 centimeters; the diameter of the calyx 1. (Writer's translation.)

Milne-Edward's preceding description is fairly comprehensive, and a very complete description of the external characters of *H. cassedayi* is given by Beede. (See synonymy above).

Internal characters.—(Pl. 13, Figs. 15-20.) As may be seen in Fig. 20, the internal structure of *H. cassedayi* during the neanic period is entirely different from that characterizing the later stages. In these youthful portions of the corallum the primary septa, of which 13 are visible in the section, extend to the center, where their ends join. The cardinal and counter septa are so nearly continuous as to strongly suggest the original "axial septum" of Carruthers; as though these two, existing first as a single septum stretching across the diameter of the calyx, had not yet broken apart to form the cardinal and counter septa. If this is actually the case the early development of *H. cassedayi* must be much retarded, as the section is from a relatively late neanic stage. The position of the cardinal fossula can be determined only from the location of the cardinal septum. The phyllotheca characterizing the genus *Hapsiphyllum* is not formed until after the neanic period, when it arises through the further insertion of septa, and the bending and fusing of the inner margins of these later-comers. The septal acceleration emphasized by Grabau as a character of the genus is already perceptible in the neanic stage, there being 6 septa in the counter quadrants and only 5 in the cardinal quadrants. Tabulae and dissepiments appear to be absent.

With the continued insertion of septa during the ephebic stage the appearance of the cross-section of the corallum is entirely transformed (Figs. 16-19). The 23 septa of Fig. 19 have produced a phyllotheca which completely walls off an elongated cardinal fossula. The cardinal septum is rapidly receding. In the counter quadrants the development of secondaries is nearly complete, and they are characteristically fused with the adjacent primaries. Secondary septa have not yet developed in the cardinal quadrants, and their formation is considerably retarded, as is evidenced by Fig. 18, in which they may be detected as marginal rudiments. The counter quadrants continue to be accelerated over the cardinal quadrants until the adult number of 24 primary septa is achieved. Fig. 15, a section from a mature stage, exhibits the septal pattern of the calyx, with all secondary septa developed. The characteristic "key-hole" shape of the cardinal fossula, and the full development of its enclosing phyllotheca are here well shown.

Remarks.—The external characters of *H. cassedayi* are distinctive, and have been described frequently and accurately; the extensive synonymy is therefore somewhat surprising. In part this may be traced to the apparent variability shown by this species in the development of a spinose or smooth exterior; in part it is evidently due to lack of familiarity with the literature. It is to be noted that all the species grouped in the synonymy are from the same geologic horizon, and from a relatively restricted area. A seeming ex-

ception is *Zaphrentis calcariformis* Hall, which is assigned by its author to the Corniferous (Onondaga) limestone of the Falls of the Ohio. Worthen, however, states that Hall erred in so assigning it, and that the type is actually from the Warsaw division of the St. Louis limestone. This same formation is also the source of the Milne-Edward's holotype of *Z. cassedayi*, and of the holotypes of the other species here considered identical with *H. cassedayi*.

In keeping with this marked limitation in the horizontal and vertical range of these forms, it may be further observed that *Z. prona* Milne-Edwards, as evidenced by that author's description, differs from *H. cassedayi* only in the absence of epithecal spines. The septal apparatus is stated to be identical in number and disposition in both forms. Aside from the ease with which such delicate and exposed structures as exothecal spines may become obliterated, their presence or absence, unaccompanied by other variation, seems a doubtful basis for specific differentiation. The same considerations are equally applicable to *Z. calcariformis* Hall. The description of this species is in every respect comparable to that of *Z. cassedayi* Milne-Edwards, except for the absence of external spines. Worthen's hypotype for *Z. calcariformis* (Pl. 9, Figs. 18, 25) appears to be a *Hapsiphyllum cassedayi* the exterior of which is smooth, either as a result of erosion or of mutation. *Zaphrentis ulrichi* is stated by Worthen to differ from *Z. calcariformis* Hall only "in its compressed and more rapidly expanding form." These again are characters hardly of specific worth when unsupported by any endothecal differences. Variations in the rate of expansion and the degree of attenuation of the corallum may be observed in profusion among individuals of any species of which a considerable number are compared.

Hypotypes. 26600, Walker Museum, University of Chicago; 2558, Illinois State Museum.

Horizon and localities.—"Corniferous" (?) limestone, Falls of the Ohio; Warsaw division of the St. Louis group, Spergen Hill, Washington County, Georgetown, Floyd County, Lanesville, Harrison County, Paynter's Hill, Bedford, Harrodsburg, Bloomington, Elletsville, Stinesville, and Romona, Indiana; Coalsburg, Kentucky.

Genus **Clinophyllum** gen. nov.

Pl. 9, Figs. 12-14; Pl. 12, Figs. 17-21.

Derivation of name: κλίνω—lean, φύλλον a leaf.

Description.—Corallum medium-sized or small, cornute. Calyx inclined at a high angle to the long axis of the corallum. The floor of the calyx is formed from a smooth, steeply tilted tabula, which may be nearly plane or arched downwards in a broad funnel shape. Septa short, proximally thick, but tapering rapidly to an edge. The counter septum is the largest in the calyx, and its position and prominence is emphasized by a lateral gap between it and each of the adjacent primary septa. In mature individuals these counter gaps are each occupied by a small, pinnately placed secondary septum. In the type species the two secondary septa thus located are the only members of their septal cycle, all the other septa being primaries. The cardinal septum is second only to the counter septum in prominence. It arches above its

neighbors, and extends farther toward the center of the calyx than any other septum of the cardinal quadrants. The alar septa are distinctly smaller than the other primaries, and occupy alar pseudo-fossulae.

Internal characters. -In the early stages the septa are radially symmetrical, and reach to the center. With expansion of the corallum they become marginally retracted, and the central area becomes open. As growth continues the cardinal and counter septa become greatly thickened and strongly differentiated from the remaining primaries. These latter, although very unequal, are of approximately the same order of magnitude. Tabulae are not numerous, but are very complete, and are placed at the same high angle which characterizes the floor of the calyx. All the more mature portions of the corallum are included in the calyx, within which the radial arrangement of the septa is replaced by a radio-pinnate disposition. Dissepiments are absent.

Remarks.— The genus *Clinophyllum* is unusual in the pseudo-pinnate arrangement of the septa of the counter quadrants, which is in a vertical rather than a horizontal plane; in keeping with this inverted character is the strong development of the counter pseudo-fossula. The acceleration of the counter quadrants is evidenced in the type species by the fact that the only secondary septa are inserted adjacent to the counter septum. The high angle of inclination of the tabula forming the floor of the calyx is further diagnostic of the genus.

A calyx steeply inclined to the long axis of the corallum is a not uncommon feature of the mature stages of the many corals. In *Clinophyllum* this trend has become dominant early in the development of the individual, and is apparently responsible for the other peculiarities of the genus. (Compare the theories of Yakowlew and Weissermel).[28]

Clinophyllum chouteaunse (Miller)

Pl. 9, Figs. 12-14; Pl. 12, Figs. 17-21.

Zaphrentis chouteauensis Miller, Adv. Sheets, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 10, pl. 1, figs. 11-12, 1891.

Zaphrentis chouteauensis Miller, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 620, pl. 1, figs. 11-12, 1892.

Zaphrentis chouteauensis Keyes, Missouri Geol. Surv., **4**:112, 1894.

Description.—Miller's original description reads:

Corallum below medium size, slightly curved, rapidly expanding at the sides, and tapering to a point at the base. Usually constricted immediately above the base, and also having shallower constrictions on the convex side, caused by intermittent growth. Epitheca thin. Calyx subovoid, nearly parallel with the long axis of the corallum or standing almost upright; it constitutes nearly the whole of the corallum, for there is only a small point below it. Septa unequal, a few small ones near the margin of the calyx, but they soon fade away; primary septa short and thick in the expanded part of the calyx and coalesce as they approach the base of the cup. There are thirty-two primary septa in the calyx of the specimen illustrated. . . a much smaller specimen has only twenty-four, and larger specimens probably have as many as forty. Septal fossette large, occupying the central part of the calyx and projecting toward the concave side

28 Yakowlew, N. N., op. cit.; Weissermel, W., Zeitschr. Deutsch. Geol. Gesell., **49**:865-888, 1897.

of the corallum. This species is distinguished by its lateral expansion, upright calyx, and short, thick, coalescing septa.

Miller's interpretation of the structure of his species appears to be erroneous in several respects. Since neither the cardinal nor the counter septa are aborted at any stage of development, the formation of a true fossula is impossible. The pseudo-fossula visible in the calyx is occupied by the counter septum, a fact which is verified by an inspection of the rugae. Miller's description of a cardinal fossula rests upon the assumption that the entire calyx is involved in the production of this structure, which would thus be walled by the central tabulate area and projected toward the concave side by the slope of the calicular floor. This interpretation is disproved, however, by the internal structure, which in the mature stages is devoid of any suggestion of a fossula. The survey of a considerable number of individuals reveals specimens in which the floor of the calyx is not infundibulate, but remains nearly plane tabula on to which the primary septa project for a short distance before their termination.

The alar septa are slightly recessive within the calyx, and the development of small gaps between each of them and the adjacent septa produces an impression of alar fossulae. The structures so formed are confined to the wall of the calyx, and disappear at its floor, being in this respect entirely analogous to the counter pseudo-fossula. The counter septum is the largest in the calyx, and in mature individuals there is a secondary septum on either side of it. The cardinal septum is the largest in the cardinal quadrants; its situation is not marked by any depression nor by lateral gaps. The remaining septa of the cardinal quadrants are uniformly spaced, subequal in size, and radially disposed.

Internal characters.—In the earlier ontogeny of *C. chouteauensis* the septa are radially symmetrical and extend to the center of the corallum. In occasional individuals there is a weakly developed cardinal fossula in sections younger than the ephebic stage, beyond which it disappears. As a rule the protosepta are not markedly distinguished from the other primaries during the neanic stages. The youngest section obtained (Fig. 21) exhibits 12 moderately thick septa; dissepiments appear to be absent. During the ephebic period (Figs. 19-21) the elongation of the septa proceeds less rapidly than the expansion of the corallum, so that the septa are pulled toward the margin and a central open space formed. In this stage the sub-equality of the septa is broken by differential thickening of the cardinal and counter septa, which eventually become more than double the width of the next largest septa. The development of broad, highly inclined tabulae first becomes conspicuous in the ephebic period. These completely partition the corallum, and are of considerable thickness, as may be seen from the tabular intercept visible in Fig. 18, Pl. 12. The tabulae dip in the direction of the cardinal quadrants, and the septa of these quadrants fuse onto the tabular surface in a manner similar to that exhibited in the calyx.

Hypotypes.—9679 Walker Museum, Univ. of Chicago.

Horizon and locality.—Chouteau limestone near Sedalia, Mo.

Family *Cyathaxonidae* Milne-Edwards and Haime

Corallum having the septal apparatus well developed; the septa extend without interruption from the base to the summit of the visceral chamber, leaving between themselves cavities which are open throughout their height, presenting neither traverses, nor tabulae, nor synapticulae. The septa of the first order are not notably more developed than the others, and do not form a quadri-branchiate cross as among the majority of the *Stauridae*.

By the great development of the septa and the absence of the endotheca this little group recalls the family of the *Turbinolidae* among the *Madreporaria aporosa*, and it appears to be the representative of these among the *Madreporaria rugosa*. Among the *Stauridae*, the *Cyathophyllidae*, and the *Cystiphyllidae* the endothecal system is always well developed. (Writer's translation).

Genus *Cyathaxonia* Michelin

Michelin, Icon. Zooph.: 258, 1846.

Description.— Corallum simple, free, artfully pedicellated, and having the form of an elongated and curved cone. Epitheca complete. A well developed septal fossula, situated on the side of the greatest curvature of the corallum. Columella styliform and markedly projecting. Septa smooth, numerous, and the majority extending to unite with the columella. (Writer's translation).

Cyathaxonia tantilla (Miller)

Pl. 9; Figs. 15-17.

Zaphrentis tantilla Miller, Adv. Sheets, 17th Rept. Indiana Dept. Geol. Nat. Res.: 11, pl. 1, figs. 23-24, 1891.

Zaphrentis tantilla Miller, 17th Rept. Indiana Dept. Geol. Nat. Nat. Res.: 621, pl. 1, figs. 23-24, 1892.

Zaphrentis tantilla Keyes, Missouri Geol. Surv. **4**:111, 1894.

Cyathaxonia minor Weller, Bull. Geol. Soc. America, **20**:270, pl. 10, figs. 14-17, 1909.

Description.—Miller's original description is:

Corallum very small, moderately curved, elongate, turbinate, regularly enlarging and acutely pointed at the base. Surface bearing a few shallow constrictions of growth. Epitheca thin. Calyx very deep, and mouth transverse, not oblique to the long axis of the corallum. Septa short, equal and uniting in the center of the cavity. The calyx is so deep that I have been unable to see the fossula by looking into it. Where, however, the wall of the calyx is broken away, I have observed a subcentral depression that indicates the position of a small fossula on the convex side of the corallum. There are 24 septa in the specimen illustrated, which is .1 of an inch in diameter; a little larger specimen has thirty septa.

This species is distinguished by its minute size, elongated form, and deep, transverse calyx.

The tiny calyx of *C. tantilla* is almost invariably filled with deposits of sediment, and the details of the septal arrangement within the calyx obliterated. The minuteness of the structures defies cleaning by any of the common methods. In such calices as could be observed there was no evidence of a fossula. The septa are undifferentiated, radially disposed, and exist as low ridges on the inner wall of the calyx. They extend downward nearly vertically until they are obscured by the depth of the calyx. The columella projects at least two-thirds of the height of the calyx, and increases regularly in diameter as it approaches the calicular floor.

Internal characters.—In sections taken near the tip, the columella is revealed as a broad structure occupying the central half of the corallum. The septa are short and thick, and without exception extend to the columella, with which they fuse. They are entirely radial in arrangement, and undifferentiated. There is no suggestion of fossula, tabulae, nor dissepiments. In sections obtained from progressively older portions of the corallum, the columella is observed to decrease steadily in diameter. In the ephebic stages the septa fail to reach the columella, which thus becomes an isolated central structure. The septa of this period have become differentiated into two distinct cycles. Each alternate septum has become about one-third longer than its neighbors, and has increased slightly in thickness. The radial orientation is still perfectly preserved. In sections taken above the base of the calyx the septa are again undifferentiated, and exist as short, sharply edged marginal ridges.

Remarks.—In describing *Cyathaxonia minor* Weller compares his species with *C. tantilla* Miller as follows: "The species is most closely alied to *C. tantilla* (S. A. M.) but is usually more curved and has less strong longitudinal costae." Weller's cotypes are essentially identical with *C. tantilla*, however, except for the "costal" difference he notes, and this latter seems to have resulted solely from the poorer preservation of the exteriors of his specimens, as compared with Miller's.

The absence of a fossula in *C. tantilla* is at variance with the characters designated for the genus *Cyathaxonia*. The strong development of the septal apparatus, the absence of tabulae and dissepiments, and above all the presence of a salient columella, seem to justify its position in this genus.

Hypotypes.—38042, Walker Museum, University of Chicago.

Horizon and locality.—Chouteau limestone near Sedalia, Missouri; Kinderhook (Fern Glen) limestone, Louisiana, Missouri.

Genus **Crassiphyllum** gen. nov.

Pl. 9, Figs. 9-11; Pl. 12, Figs. 12-16.

Derivation of name: crassus—thick; *φύλλον*—a leaf.

Genotype.—*Zaphrentis declinis* Miller, 17th Rept. Indiana Dept. Geol. Nat. Res.: 621, pl. 1, figs. 25-26, 1892. Keokuk group, New Providence, Indiana.

Description.—Corallum small, straight or gently cornute. Calyx small, shallow, often broken by a rudimentary cardinal fossula and always marked by a central circular opening which is smoothly walled by the distal fusion of the septa into a phyllotheca; this latter may be reënforced by deposits of stereoplasm. The tube thus formed is continuous to the tip of the corallum. Septa of a single cycle only, nearly equal in size. Within the calyx the septa are short and proximally thick, but taper abruptly to an edge.

Internal characters.—The structure of the genus *Crassiphyllum* is extremely simple. The corallum is formed from a radial array of short, thick septa, which fuse together about a central opening extending the length of the individual (Fig. 4). Tabulae are entirely lacking, and both the central open-

ing and the interseptal spaces are unbroken throughout their length except for a few marginal dissepiments, which are usually confined to the earlier stages. There is no suggestion of a fossula anywhere in the internal structure, and the septa are consistently sub-equal and radially disposed.

Remarks.—The distinguishing characters of the genus are the absence of well developed fossulae and of tabulae; the thick undifferentiated septa of a single order, and the central opening walled by a phyllotheca. Despite the presence of a few dissepiments, this genus seems to belong naturally in the family *Cyathaxonidae.*

Fig. 4. Camera lucida drawings of serial sections of *Crassiphyllum declinis* (Miller).

Crassiphyllum declinis (Miller)

Pl. 9, Figs. 9-11; Pl. 12, Figs. 12-16.

Zaphrentis declinis Miller, Adv. Sheets, 17th Rept. Indiana Dept. Geol. Nat. Res.: 12, pl. 1, figs. 25-26, 1891.

Zaphrentis declinis Miller, 17th Ann. Rept. Indiana Dept. Geol. Nat. Res.: 622, pl. 1, figs. 25-26, 1892.

Description.—Corallum small, elongate, turbinate, more or less curved, and tapering to a point at the base. Surface with shallow constrictions, caused by intermittent growth, and finer transverse wrinkles or concentric striae. Epitheca thin. Calyx moderately oblique to the long axis of the corallum and rather shallow, margin thick. Septa nearly equal, not alternate, thick within the wall, sharp centrally, not twisted; costae thick, showing externally. Septal fossula not well developed and situated on the convex side of the corallum. There are twenty-four septa in the circumference of a calyx .4 of an inch in diameter.

This species is distinguished by its elongate, turbinate form, coarse sharp septa, and wide costae.

The "costae" mentioned by Miller in his description above are not true costae, which are essentially unknown among tetracorals. In *C. declinis* the epitheca is extremely thin, and sags inward over the interseptal spaces, giving a rib-like prominence to the septa where they are thus reflected upon the exterior of the corallum. The fact that the thin epitheca is commonly removed by erosion and the interseptal spaces incompletely filled by sediments, enhances the resemblance of this feature to costae.

The cardinal septum is located upon the convex side of the corallum. In numerous individuals it may be slightly recessive in the calyx, producing a very small, shallow rudimentary fossula, but individuals are equally numerous in which there is no suggestion of such a structure, and it was probably not functional.

Internal characters.—(Pl. 12, Figs. 12-16). The cross-section of the corallum is oval, often considerably flattened. The septa, from their earliest development are sub-equal and radial, but those parallel to the long axis of the

cross-section are generally of greater length than those paralleling its shorter axis. In Fig. 16, which is from the ephebic stage, there are 17 sub-equal septa, radially arranged. The protosepta cannot be distinguished, either by size or by position. The phyllotheca surrounding the open center of the corallum is completely developed, and there are indications of several rows of dissepiments. Each of the short thick septa shows clearly a light central line marking its center of calcification (Fig. 4). The trace of these lines indicates that the septa tend to fuse into about four groups, such fusion being especially pronounced in the more compressed areas of the corallum. The interior of the corallum exhibits little change from early youth to maturity, (Pl. 12, Figs. 13-16), beyond an increase in the number of dissepiments. In Fig. 12, a section taken acros the base of the calyx, the septa project above the phyllotheca and terminate in a sharp edge. They are markedly thick peripherally, and retain their sub-equality, but conspicuously lack the radiopinnate orientation characteristic of most tetracorals.

Cotypes.—6615 Walker Museum, Univ. of Chicago.

Horizon and locality.—Keokuk Group, New Providence, Ind.

C.—Phylogeny and Distribution

Although an intensive phylogenetic study is beyond the scope of the present paper, a brief general survey of the relationships of the forms studied may be appropriately included.

From both stratigraphic and morphological considerations, it is apparent that in seeking the relatives of the *Zaphrentidae* we need look only laterally and backward. All the members of this family which have been here considered became extinct by the close of the Mississippian, and the family itself is unknown in strata younger than Pennsylvanian. A general phylogeronticism of the corals might be deduced from the remarkable variety of mutations found in the Chouteau (lower Mississippian) formation.

In the morphological development of these forms there is an anticipation of this approaching end. All are marked by a stubborn adherence to ancestral structure—the sole trend discernible among them is conservatism. The distinguishing attribute of the genus *Triplophyllum*, its alar fossulae, is not a structure arising in anticipation of profound modifications, but a primitive characteristic found in the ontogeny of all tetracorals, and here retarded to become a feature of the adult. The genus *Neozaphrentis* even more strictly recapitulates older types. The strong development of the counter septum is again the result of retardation, and the eccentric position of the cardinal fossula has been suggested as an indication of racial senility. The genus *Homalophyllum* likewise owes its characteristically flattened corallum to the inheritance of an ancestral modification, a conclusion borne out by the ancient type of endothecal structure exhibited by its species.

Among the Devonian members of the genus *Triplophyllum* may be mentioned the type species, *T. terebrata* (Hall), and *Zaphrentis edwardsi* Nicholson; the lateral range of the genus is indicated by the probable inclusion here

of *Zaphrentis griffithi* Milne-Edwards and Haime, from the Carboniferous of England, and *Hapsiphyllum altiseptum* Grabau, from the Carboniferous of China, is possibly actually a Triplophyllid.

Homalophyllum ungula (Rominger) and *H. herzeri* (Hall) have already been suggested as ancestral to *H. calceola* (White and Whitfield), and a possible Silurian ancestor of this genus exists in *Halophragma calceoloides* Lds.

That the *Hapsiphyllidae* were widespread during the Carboniferous is demonstrated by the numerous European forms and the many species described from China by Grabau. A close relationship between the *Hapsiphyllidae* and the *Zaphrentidae* seems evinced from the fact that species may be found in either genus which essentially combine the characters of both families, an especially close relationship being discernible between the genera *Triplophyllum* and *Hapsiphyllum*. The *Hapsiphyllidae*, being younger and more progresive in structure, are suggested as an offshoot of the *Zaphrentidae*.

The affinities of *Clinophyllum* are uncertain, and its position in the *Zaphrentidae* is purely tentative. The absence of a true fossula is sufficient to exclude it from this group, yet on the basis of its other morphological characters it seems most closely related to the *Zaphrentidae*.

The numerous Carboniferous representatives of the *Cyathaxonidae* have an unusual member in *Crassiphyllum*. The general morphology of the genus leaves little doubt as to the propriety of its inclusion in the *Cyathaxonidae*. Its structure, however, is peculiar in that the columella usually exhibited by the members of this family has here been replaced by a phyllotheca.

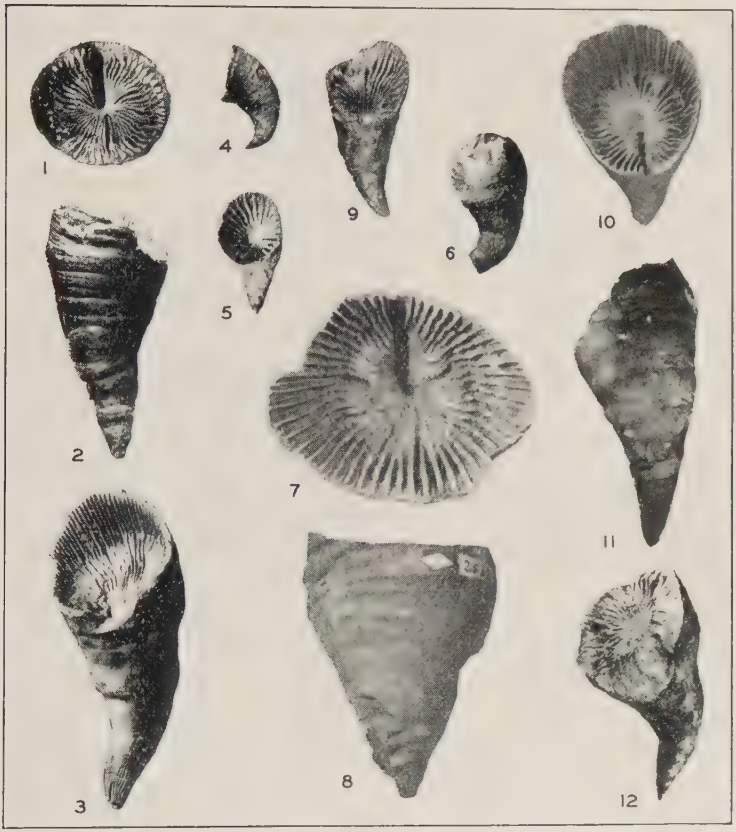
The range during the Mississippian of the species considered in the preceding pages is shown in Fig. 5.

University of Chicago,
Chicago, Ill.

	IOWA SERIES									CHESTER SERIES						
	Kinderhook			Osage		Merimac				Low. Ches.		Mid. Ches.		Upper Chester		
	Louisiana	Hannibal	Chouteau	Burlington	Keokuk	Warsaw	Spergen	St. Louis	Ste. Gen've	Renault	Paint Creek	Golconda	Glenn Dean	Vienna	Menard	Clore	Kincaid
Triplophyllum centralis				*	*												
T. dalii				*	*												
T. cliffordanum			*														
T. welleri			*														
T. spinulosum					*	*		*		*	*	*	*		*		
T. illinoisensis					*												
Homalophyllum calceolum				*	*												
Clinophyllum chout'ensis			*	*													
Neozaphrentis tenella				*													
Hapsiphyllum cassedayi						*	*										
Cyathaxonia tantilla			*		*												
Crassiphyllum declinis					*												

Fig. 5. Stratigraphic distribution of the species considered in the foregoing pages.

PLATE 8



FIGURES

1–3. *Triphlophyllum dalii* (M-E. & H.). Fig. 1 shows the calyx of Worthen's hypotype; Fig. 2 is a lateral view of the same specimen; Fig. 3 is a hypotype showing the curvature of the corallum.

4–5. *Triplophyllum cliffordanum* (M-E. & H.). Calicular and lateral views of Weller's hypotypes.

6. *Triplophyllum cliffordanum hespere* Grove, Cotype showing swollen aspect of upper corallum.

7–8. *Triplophyllum illinoisense* (Worthen). Calyx and convex side of the holotype.

9. *Triplophyllum welleri* Grove. Holotype.

10–11. *Triplophyllum centralis* (M-E. & H.). Fig. 10 is Worthen's hypotype, Fig. 11 another specimen showing convex side of corallum.

12. *Triplophyllum spinulosum* (M-E. & H.). This specimen is Worthen's hypotype of *Zaphrentis spinulifera* Hall.

PLATE 9

FIGURES

1–5. *Dibunophyllum spinulosum* (M-E. & H.). Fig. 2 is the holotype of *Zaphrentis chesterensis Worthen;* Figs. 3 and 4 are the cotypes of *Z. pellaensis* Worthen. Fig. 5, the calyx of a hypotype, shows the full development of three fossulae.

6–8. *Zaphrentis tenella* (Miller). Hypotypes.

9–11. *Cossiophyllum declinis* (Miller). Cotypes.

12–14. *Cossiophyllum chouteauensis* (Miller). Hypotypes. The eroded epitheca of the specimen shown in Fig. 14 permits a perception of the inclined tabulae.

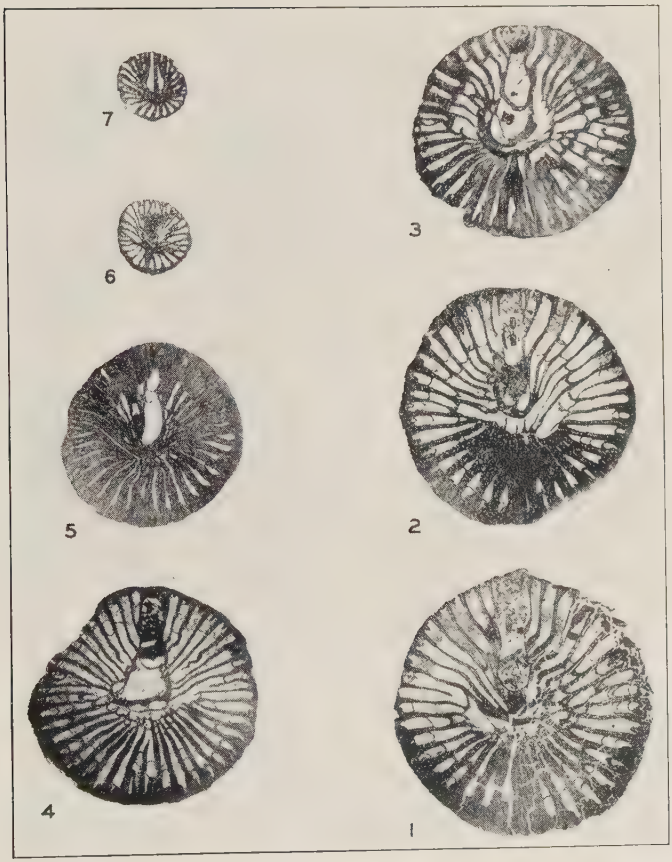
15–17. *Cyathaxonia tantilla* (Miller). Hypotypes.

18–19. *Heterophyllum cassedayi* (M-E. & H.). Calicular views of Worthen's hypotypes for *Zaphrentis calcariformis* Hall.

20–24. *Homalophyllum calceolum* (Wh. & Whit.). Hypotypes.

25. *Heterophyllum cassedayi* (M-E. & H.). Lateral view of the specimen shown in Fig. 18.

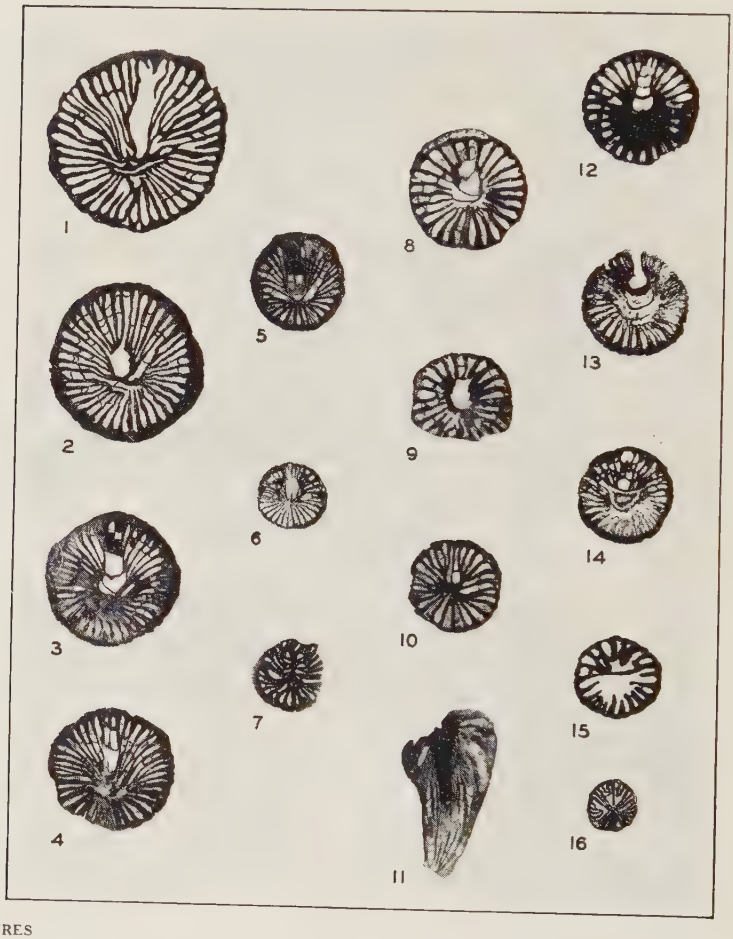
PLATE 10



FIGURES

1–7. *Triphlophyllum centralis* (M-E. & H.). Serial sections illustrating the changes in internal structure from late neanic to adult stages. x2

PLATE 11



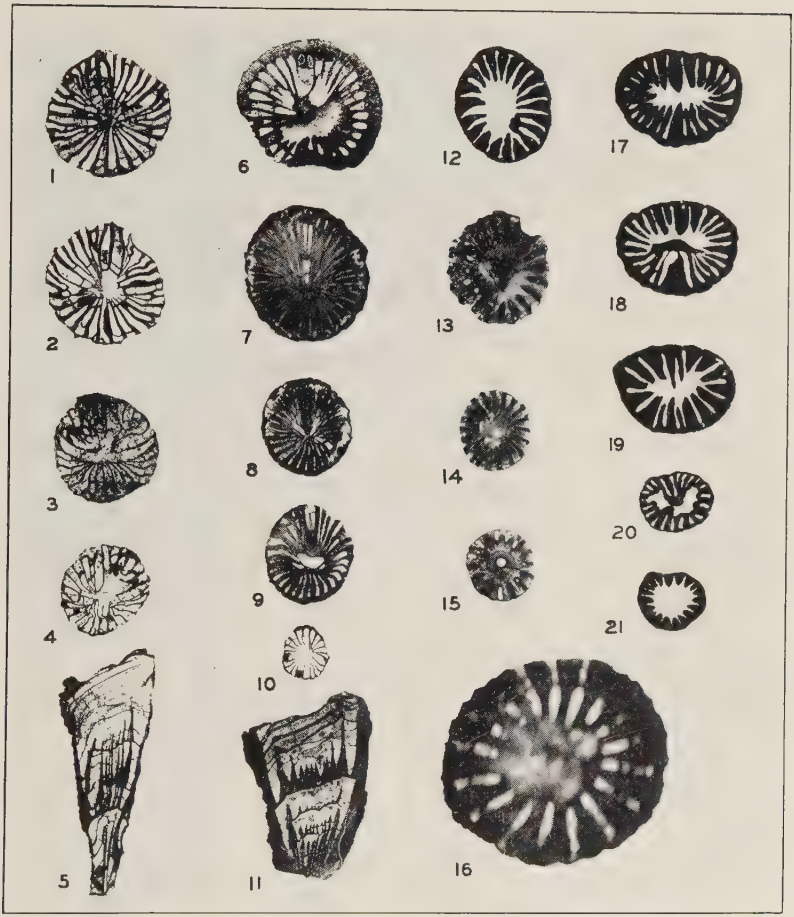
FIGURES

1–7. *Triplophyllum dalii* (M-E. & H.). The serial sections of Figs. 1-6 are magnified 1½ times; Fig. 7 is a tip section enlarged 4 times.

8–11. *Triplophyllum cliffordanum* var. *hespere* Grove. x2.

12–16. *Triplophyllum cliffordanum* (M-E. & H.). Composite serial sections from three individuals. x2.

PLATE 12



FIGURES

1–5. *Triplophyllum spinulosum* (M-E. & H.), var. α. x1½.

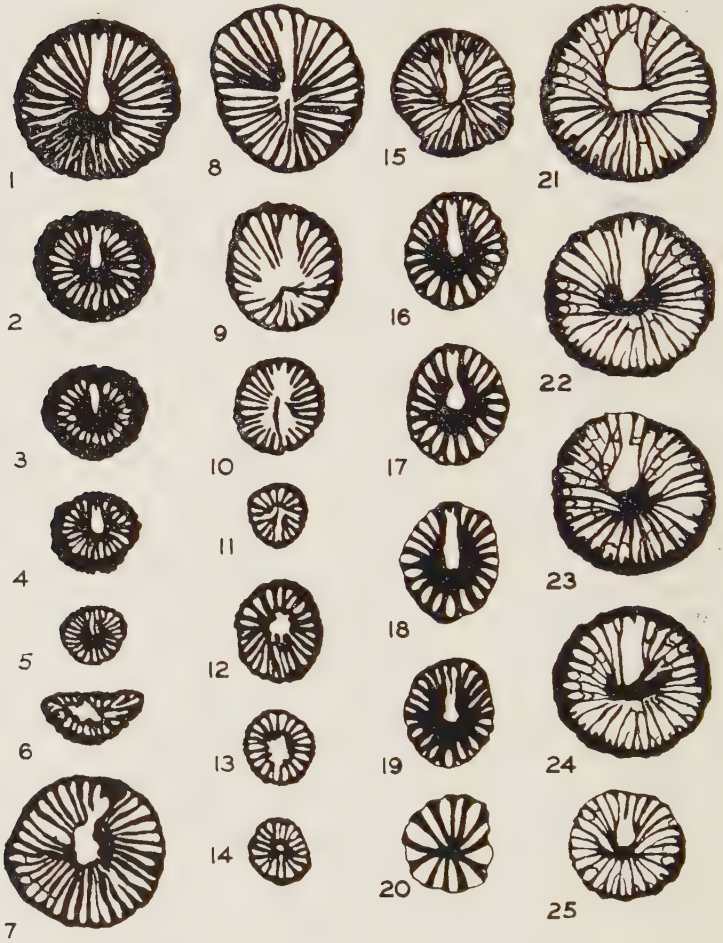
6–10. *Triplophyllum spinulosum* (M-E. & H.). var. β. x1½.

11. *Triplophyllum spinulosum* (M-E. & H.), var. α. x1½. This vertical section is shown for comparison with Fig. 5, and illustrates the uniformity of internal structure which prevails despite dissimilarity in the shapes of the coralla.

12–16. *Crassiphyllum declinis* (Miller). Serial sections, all x2 except Fig. 16, which is a tip section enlarged 12 times.

17-21. *Clinophyllum chouteauense* (Miller). x2.

PLATE 13



1-6. *Homalophyllum calceolum* (Wh. & Whit.). Figs. 1-5 are serial sections of a single individual, and are enlarged 3 times; Fig. 6 is from a neanic stage, and is x4.

7-14. *Neozaphrentis tenella* (Miller). Composite serial sections from a number of individuals, enlarged 3 times.

15-20. *Hapsiphyllum cassedayi* (M-E. & H.). All but Fig. 20 are enlarged 3 times; Fig. 20 is magnified approximately 5 diameters.

21-25. *Triplophyllum welleri* Grove. Serial sections of a cotype. x2.